Marcelo Domingos de Santis

O Problema da Explicação na Sistemática e uma Hipótese Filogenética para Dexiinae Macquart, 1834 (Diptera, Tachinidae)

The explanation Problem in Systematics and a Phylogenetic Hypothesis for Dexiinae Macquart, 1834 (Diptera, Tachinidae)

São Paulo

2021

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências Biológicas, na Área de Zoologia.

Orientador(a): Prof. Dr. Silvio Shigueo Nihei

São Paulo
2021

Ficha Catalográfica

Santis, Marcelo Domingos de

O Problema da Explicação na Sistemática e uma Hipótese Filogenética para Dexiinae Macquart, 1834 (Diptera, Tachinidae)

328 + xiii pp.

Tese (Doutorado) - Instituto de Biociências da Universidade de São Paulo. Departamento de Zoologia.

1. Diptera 2. Dexiinae 3. Explicação Científica 4. Sistemática 5. Causalidade.

I. Universidade de São Paulo. Instituto de Biociências. Departamento de Zoologia.

Comissão Julgadora:

Prof(a). Dr(a).	Prof(a). Dr(a).
Prof. Dr. Silvio Shigueo Nihei Orientador(a)	Prof(a). Dr(a).

Epígrafe

“[Darwin] introduces morphology as ‘the most interesting department of natural history, [which] may be said to be its very soul’”

The Structure of Evolutionary Theory (2002) by Stephen Jay Gould

Agradecimentos

Sou muito grato pelo constante apoio e encorajamento da minha irmã, Mara, e da minha mãe, Suely, que sempre estiveram ao meu lado. Meu mais profundo agradecimento por tudo que fizeram e fazem! Um agradecimento especial ao Francisco, “Kiko”, por todo apoio; meu muito obrigado!!

À Giovanna, ao amor da minha vida, que me apoiou, ouviu e compartilhou tantas coisas que é indescritivel a minha gratidão! Não há palavras que expressem o quanto sou grato por tudo!

Ao meu orientador Silvio Nihei, por toda liberdade intelectual e apoio que me deu desde o início da minha trajetória em seu laboratório. Por ter me apioado em idéias dentro da Filosofia da Ciência, que por si só é um grande desafio! Agradeço pela amizade e orientação em todos os desafios encontrados durante esses anos.

Ao longo desse período de doutoramento, procurei aprofundar meu conhecimento na Filosofia, mais especificamente, na Filosofia da Ciência. Com isso, passei a frequentar a Faculdade de Filosofia, Letras e Ciências Humanas (FFLCH) da USP, na qual pude conhecer e estabelecer um diálogo extremamente frutífero com várias pessoas que são uma grande inspiração para mim, cabendo-me destacar os professores Maurício de Carvalho (FFLCH-USP), João Cortese (IB-USP) e Rômulo Ferreira (UFRJ-RJ). Fica aqui a minha gratidão por todas as conversas, conselhos e aprendizagem!

Aos integrantes do Laboratório de Sistemática e Biogeografia de Insecta da Universidade de São Paulo, por toda a ajuda fornecida nesses anos de convivência. Cada um, a sua maneira, contribuiu de forma muito significativa para este trabalho. Todas as conversas, risadas e cafés sempre foram importantes demais! Gostaria de deixar um agradecimente especial ao Filipe Gudin, Rodrigo Dios, Lucas Denadai, Jorge Andino, Daniel Máximo, Deivys Moisés, Darían Redü, Leticia Baldassio, Pedro Dias e Fabio Laurindo.

Um agradecimento espécal à Leandro de Assis (UFMG) por todo diálogo, incentivo e críticas que me levaram a pensar e trabalhar de uma forma muito mais aprofundada. Agradeço demais a parceria (e paciência)!

Aos funcionários Instituto de Biociências, especialmente ao Departamento de Zoologia da Universidade de São Paulo (USP); em especial agradeço à Lúcia e Lilian por sempre estarem presentes em auxiliar em vários processos nessa caminhada.

Ao Nigel Wyatt por ter me recebido no laboratório do Natural History Museum (Londres, Inglaterra) durante meu doutorado sanduiche. O acesso a coleção, e ao material fotográfico, foi essencial para a compreensão de Dexiinae e para o desenvolvimento desta tese.

À Dra. Márcia Couri do *Museu Nacional da Universidade Federal do Rio de Janeiro*, ao Dr. Carlos Lamas do *Museu de Zoologia da Universidade de São Paulo* e à Dr. Jane Costa da *Coleção Entomológica do Instituto Oswaldo Cruz*, pelo acesso á coleção e ao empréstimo de material.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (processo 88882.333078/2019-01) pela concessão da bolsa de Doutorado e pela bolsa CAPES-Print relativo ao doutorado sanduíche.

E aos meus professores, que me introduziram as alegrias da compreensão do mundo.

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Capítulo 3

Introdução geral

A sistemática biológica estuda a diversidade da vida e inclui anatomia comparativa, taxonomia e classificação. Como agora entendemos que essa diversidade é o resultado de processos evolutivos, a sistemática também inclui a tarefa de formular hipóteses robustas sobre a história evolutiva. Filogenética, então, é o estudo da elaboração dessas hipóteses com a história dos organismos que envolve a construção de filogenias – que são geralmente representadas por árvores filogenéticas, que retratam eventos de especiação de linhagens ao longo do tempo. Com isso, a análise filogenética tornou-se um elemento essencial que unifica uma ampla gama de programas de pesquisa que investigam os padrões, e possibilitam os estudos dos processos, da evolução. Porém, o que, precisamente, a sistemática filogenética explica? Se ela se propõe a fornecer explicações, de que forma a sistemática fornce explicações? E, finalmente, essas explicações estão adequadas? Se um dos objetivos da ciência é fornecer explicações bem-sucedidas, para, assim, produzir uma teoria científica capaz de construir uma série de explicações causais nas quais explicam-se outros fenômenos (Strevens, 2013), as questões de expplicação na filogenetica serão analisadas e uma tentativa de responder a estas perguntas serão dadas.

Visto que essa tese propõe uma contribuição para a teoria, filosofia e prática da sistemática, para respondê-las, no Capítulo 1 será defendida uma conexão científico-filosófica como uma ferramenta para nosso entendimento da sistemática. Muito brevemente, a resposta aqui dada se dará da seguinte forma: quando damos uma explicação de função de determinado traço, estamos dando explicações causais extremamente compactas para o porquê desses caracteres existirem. As funções são teleológicas pois são direcionadas para o futuro, porém sem serem metafisicamente direcionadas. Assim, uma teoria da função, com o objetivo de fornecer uma explicação teleológica-causal, deve assumir o papel causal-explicativo das funções e, dessa forma, dar uma explicação causal para a existência desses caracteres (Garson, 2019). Com isso, poderemos avaliar como cada grupo de pesquisa dá a sua resposta a esta questão, para desta forma avaliarmos de uma forma filosófica/empírica qual deles estaria lidando com o melhor modelo de explicação na sistemática. Neste capitulo, será argumentado que o principal desafio no estudo da causalidade teleológica funcional é principalmente conceitual e não empírico; pois já se utilizam ferramentas as heurísticas para analisar a causalidade funcional (como a parcimônia), devemos ampliar esse conhecimento para outros campos. Sugere-se, portanto, a iluminação recíproca de diferentes campos de investigação –

como a etologia, análise funcional, ecologia, estudos moleculares e de desenvolvimento – para obtenção de uma explicação causal adequada. Com isso, dá-se maior relevância para a morfologia como uma proposta de explicação causal na sistemática filogenética. Em contrapartida, a análise molecular (com sua inferência probabilistica) tem valor mecânicos extremamente valiosos, porém com limitações ontológicas inerentes de sua propriedade de ser a menor unidade retentora de informações da biologia. Adicionando-se que a morfologia enquadra-se como os 'interadores', e são, assim, as unidades fundamentais da seleção, enquanto os replicadores, como os dados moleculares, não pertencem a essas unidades (ao menos diretamente). Assim, brevemente, será argumentado que podemos considerar que as únicas informações que podemos obter para a análise funcional potencialmente úteis para a sistemática, não são de replicadores, mas de 'integradores' (formas e funções), com a função do material genético de melhorar nossa compreensão mecânica dos organismos.

A parte empírica é o foco dos Capítulos 2, que trata-se de uma hipótese filogenética para a subfamília Dexiinae (Tachinidae). A subfamília é distribuída mundialmente (Cantrel & Sabrosky 1989, Crosskey 1976, Guimarães 1971, Herting & Dely-Daskovits 1994, O'Hara & Wood 2004, O'Hara & Cerretti, 2016; O'Hara et al., 2020) e contém 1495 espécies em cerca de 287 gêneros (O'Hara et al., 2020). Utilizando 152 espécies de 107 gêneros, representando todas as 12 tribos atualmente reconhecidas, e com um total de 212 caracteres morfológicos do ovo (2), larva de primeiro ínstar (30), morfologia externa adulta (97, excl. Terminália), terminália feminina (19), terminália masculina (59) e espermateca (2), esta hipótese foi realizada. Em uma aspecto geral os resultados apontam para a confirmação de que Dufouriini, não pertence a Dexiinae nem a Phasiinae, e de acordo com os resultados aqui obtidos, as seguintes tribos são retiradas de Dexiinae: Oestrophasiini, Freraeini e Dufouriini, constituindo agora sua própria subfamília, Dufouriinae (status revalidado) sendo um grupo irmão de Phasiinae. O outro resultado principal, é que o Voriini *sensu lato* é polifilético, e para propor esta tribo como monofilética, revalidamos as tribos Campylochetini **tribe rev**., Eriotrichini **tribe rev.,** Phyllomyini **tribe rev**., Thelairini **tribe rev.** Spathidexiini **tribe rev.** and Wagneriini **tribe rev**.; Voriini *sensu stricto*, de acordo com a nova classificação, é agora monofilético. Eutherini, Epigrimyiini e Imitomyini dubiamente classificador ora em Dexiinae, ora em Phasiinae, tiveram seu posicionalmte robustamente suportados em Dexiinae para as duas primeiras tribos e Phasiinae para a últuma. Por outro lado, Doleschaliini e Rutiliini foram recuperados em Dexiini e são, seguindo essa hipótese filogenética, colocados em sinonímia com Dexiini. As tribos Dexillini, Theresiini, Trichodurini, Trixodini, Prosenini e Zeliini, são confirmadas como inválidas e são consideradas sinônimos de Dexiini.

Já no capítulo 3, uma breve revisão cronológica da história dos Dexiinae Neotropicais, a partir dos cientistas e coletores que trabalharam com essa subfamília, será discutida. Com base em uma revisão da literatura, será discutida sua história em quatro períodos: época pré Linneana do séculos XVI e XII, início do século XVIII, século XIX e primeira metade do século XX. Até a primeira metade do século XX a ênfase estará voltada para os dipteristas europeus e norte-americanos. Posteriormente, com a aparição dos primeiros dipteristas sul-americanos, a ênfase será direcionada a eles. Finalmente, algumas notas bibliográficas serão fornecidas para o tcheco Dominik Bilimek, um pouco conhecido coletor do século XIX e Fritz Plaumann, um conhecido imigrante alemão que coletou no Brasil durante o século XX.

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Capítulo 1

Phylogenetic Systematics and Scientific Explanation: the Explanation Problem in Systematics

SYSTEMATIC PHYLOGENETICS AND SCIENTIFIC EXPLANATION: THE EXPLANATION PROBLEM IN SYSTEMATICS[1]

1. Introduction and the demarcation of the problem[2]

One of the goals of science is to provide an understanding of the world around us. Scientists and laypeople often regard understanding as one of the most important and valued products of scientific research. We seek explanations because they provide us with information and convey an understanding of a particular subject or fact. Successful explanations are attractive because they provide us with an understanding of what they should explain, contributing to our understanding of nature (Salmon, 1998). Thus, to understand a scientific theory is to be able to construct a series of potential explanations in which a theory explains ea xpected particular phenomena (Strevens, 2013). Therefore, there is no way for scientific understanding that does not go through a scientific explanation.

Usually, in making an explanation, we seek to answer why-questions: “Why did organisms share extraordinary similarities in molecular composition?” We do this by connecting the effect (extraordinary similarities in molecular composition) with the cause (because all contemporary life on earth descends of a last universal common ancestor). Thus, in many cases, to explain a fact is to identify its cause. We then seek causal understanding because our understanding of the world through causal concepts allows us to experience the world as structured by causal connections between phenomena or facts (Faye, 2014).

To achieve the goal of a successful explanation, we have at our disposal several models of scientific explanation. One of them is the classic model of explanation, which by the way did not consider causation as important. This model is Hempel's (1965) Deductive-Nomological explanation, that states that a particular event is a valid deductive argument whose conclusion states that the event to be explained occurred, and this conclusion is known as the *explanandum* statement. Its premises - collectively known as the *explanans* - must include a statement of at least one general law that is essential to the validity of the argument - that is, if

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[1] Algumas sessões deste capítulo encontram-se publicadas como artigos derivados diretamente deste ensaio: (1) Santis, M.D. 2020. Scientific Explanation and Systematics. *Systematics and Biodiversity*, 1-10; (2) Santis, M.D. 2020. Teleology and Biology: a defence of teleological thinking in biology. *Filosofia e História da Biologia*, (15): 61-78; (3) Santis, M.D. 2020. Popper as a process: revisiting the appropriation of the Popperian philosophy by the cladists during the 'systematics wars'. *Arquivos de Zoologia*, 51: 13-20 e (4) Santis, M.D. 2021. Misconceptions About Historical Sciences in Evolutionary Biology. *Evolutionary Biology*, 48: 94–99.

[2] This general introduction will present, very briefly, some of the straightforward ideas that will be scrutinized throughout this essay. Accordingly, some vague sentences will, hopefully, make sense in later sections.

that premise were deleted and no other changes were made to the argument, there would be no way to be valid anymore. It received several criticisms, for instance, this thesis proposes a so strict and narrow definition of explanation, which applies to only part of the physical sciences (Faye, 2014); the nomological-deductive model of explanation seems to be useful only in those cases in which we can consider the *explanandum* event as part of a very isolated, and well-defined idealized situation. During the 1970s, Hempel's (1965) thesis was set aside, giving rise to causal explanations models, for instance, that of Salmon (1984) who argues that a causal process is a physical process. According to Salmon: "[T]he underlying causal mechanisms hold the key to our understanding of the world" (Salmon, 1984: 260). The other central theory of causal explanation is that of Woodward (2003), which is an "interventionist" thesis. Basically, an explanation is obtained when there is a relationship between some variables X and Y that is causal if there was an intervention that would change the value of X suitably, wherein the relationship between X and Y does not change and the value of Y changes. e.g., the cause would be an explanation if the effect were manipulated, which would also change. We come to the conclusion that understanding is achieved when, for example, we investigate the mechanism of a mechanical clock, seeing how each part works in relation to the explanation of all the other parts. The ability to provide a causal description of how springs and gears work is our understanding of this phenomenon.

As this essay will argue matters inside biology one may wonder where does biology enter this scenario? Clearly, biological and philosophical reflections on the nature of causation in living systems have a long history, dating since Aristotle's four causes (see section 4.1), but contemporary notions of evolutionary causation have been broadly shaped by Ernst Mayr (1961). He developed a distinction (divorced from all the philosophical discussion based on physic) that set two different causes in biology: proximate causes, as current causes of phenotypic variation, like physiology and development; and ultimate causes as historical causes, like genes and natural selection. While recently, this notion has been seriously questioned (e.g., Laland et al., 2011) in relation to, mainly, questions related to reciprocal causation; his ideas still survives and marks the starting poinit for philosophers and biologists alike (Uller & Laland, 2019). The modern debate on causality in biology is centrally developed on three themes: the aforementioned proximate versus ultimate causes, the alleged existence of top-down (and bottom-up, as distinct from intra-level) causality and the nature of functional explanations (Pigliucci, 2019). Yet, this issues are not fully appreciated by biologists, and we may postulate some reasons as the complex literature on causation, and on the nature of causality itself. Thus, as argued by Uller & Laland (2019: 6): “Despite the central role of the nature of causation in evolutionary biology, the outstanding issues are rarely addressed. Evolutionary biology textbooks, for instance, hardly ever cover this topic, and such analysis as exists is dominated by philosophers of science. To biologists, at least, the literature on causation in biological systems may appear idiosyncratic and poorly connected to evolutionary theory.” Of couse, as will be showed herein, the broad problem of the nature of causality itself, is very difficult for every scientist and philosopher; however, it underpins much, if not all, of the experimental and historical sciences, even if it is hard to imagine how direct input from the causality would be helpful for those scientists. What the present essay aims to do is try to show a productive dialogue between biologists and philosophers of science; this will be done by scrutinizend the formal thesis of causality that were mostly based on physics, in order to point for resolutions, new directions and interpretations to these challenging issues in biology.

Hence, one of my main goals in this essay is to inject new life into the explanation-causality-teleology debate and show why it is so essential for thinking about these big problems in philosophy and science so that we can be able to illuminate some areas of research, in this particular case, about evolutionary biology and, as a consequence of one of its subfields, Phylogenetic Systematics. So, what exactly is an explanation? And about causation? And even, what good teleology is for? What about Systematics? How these questions can be answered? Is there a practical (and valid) model of explanation in Systematics? If not, then what model could work? These questions will be addressed properly in this essay, and for that, this survey will have the following structure that I have broken in four main parts: first, I will give a background and foundations of explanations in cladistics, where I will scrutinize how explanations are dealt in this discipline and I will argue that no theoretical or operational model exists for phylogeneticists; afterward, I will show that scientific explanation is our cognitive way to have understanding, and I argue that causation is one of the main ways achieving understanding in phylogenetics. Then, I will show, and explain, how the main thesis about explanation and causality are structured; the reader could have the impression that philosophers are hopelessly divided on the nature of explanation, but I argue that this is not really the case, because we have advanced since the early works from Hempel and Popper, and reached some straightforward conclusions: the nomological-deductive model is fatally flawed (and should be dropped) and causation is a way to avoid these errors and misconceptions; and finally, I should argue for the unique character of biology, and specially evolutionary biology: that teleology explanations (or functional analysis) are licit and legitimize our way to give evolutionary explanations (in a way that none of those philosophers of science, with physical sciences in mind could offer) and systematics should follow this path if this discipline is going to have any **explanatory depth** (*sensu* Garson, 2019).[3]

What I am proposing here is a novel approach to reach an understanding of systematic phylogenetics. In this way, following what philosophers of biology have emphasized (Brigandt, 2013), I will examine how various explanations operate in the dynamic process of the generation and application of scientific knowledge. Therefore, when we give a function explanation of particular trait, we are giving extremely compact causal explanations for why those traits exist. Functions are teleological because they are forward-directed, however without being metaphysically directed. Thus, a theory of function, with the aim to give a **teleological-causal explanation**, should take the causal-explanatory role of functions, and in this way, we can give a causal explanation for the existence of traits (Garson, 2019). It is widely recognized that both mechanistic and functional explanations are understood as causal explanations (Ayala, 2016). The evidence from philosophy and psychology (for instance, see Lombrozo and Gwynne (2014)) suggests that functional explanations differ from mechanistic explanations by the following: "…mechanistic explanations invoke proximate causal processes directly, functional explanations do so indirectly" and "functional explanations are to some extent mechanism-independent, and they have a distinct developmental and cognitive profile" (Lombrozo & Wilkenfeld, 2019). Alongside the difference lies in their causal commitments, with functional explanations being cognitively privileged in the biological sense (mainly in adaptation explanations). It is hoped that Systematics will reach a new sound philosophical foundation so that it can rise in a new life, both philosophically and empirically. When we overcome some overpassed philosophers, namely, Popper and Hempel, then we can begin to accomplish this goal. Finally, as stressed by Williams (1992), biologists must necessarily have a philosophical position about some important themes, and Williams cites the concept of causality and the nature of explanation. If this essay is going to have any virtue, is that will help systematists to make this position clearer (or even definable).

The following strategy will be our guide to answer properly all these questions: (1) I will first scrutinize how explanation is currently dealt in systematics, and (2) I will argue that in its present form it cannot give positive guidelines for systematists; later, (3) I will show all of the main thesis about causality and explanation that exists within the philosophy of science

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[3] As will be detailed later, this idea holds that function attributions act as causal agents by their special explanatory role (as in the case of teleology).

and along with this exposition, search for the more reliable, workable and best-developed model; afterwards, (4) I will point that only two seems to be the best fitted: the interventionist approach of Woodward and the causal-mechanical of Salmon; finally, while arguing that neither of those models is workable for the evolutionary biology, (5) I will point that the teleological propriety of the ‘descent with modification’ of Darwin must be added for models currently developed for philosophy of biology. From this argumentation onwards, (6) I will develop how this model of explanation for evolutionary biology works for systematics.

2. Systematics and Explanation

2.1. Hennig on causation and Phylogenetic Systematics

Phylogenetic analysis has become an essential element unifying a broad range of research programs investigating the patterns and processes of evolution. Since we now understand that this diversity is the result of evolutionary processes, systematics also includes the task of elaborating reliable hypotheses about the evolutionary history. This is made from the patterns of lineage-branching produced by this evolutionary history of life on the basis of observed patterns of sameness and difference in the characteristics of taxa using agreed upon, and rationally justified principles of inference (Wiley & Lieberman, 2011). Unlike the physical and chemical sciences, in which explanations aim to be predictive with respect to spatiotemporally invariant laws, phylogenetic analysis deals with a singular history of events (Brooks, *et al*. 2007), for example, historical narratives with its contingencies.

The German entomologist Willi Hennig, was the founder of phylogenetics systematic or cladistics, and his argumentation eventually led to a revolution in taxonomic thought, although its impact was only fully realized when they became widely known outside Germany, largely through translation into English (Hennig, 1966). Hennig's vital contribution to modern systematics was the combination of emphasizing that phylogenetic hypotheses can only be based on shared derived characteristics and he made provision of a methodology for phylogenetic analysis based on this principle. Phylogenetic Systematics, a discipline of evolutionary biology, seeks to propose classifications (reflecting the evolutionary process) with a more objective method for the elaboration of a hypothesis of the evolutionary history of groups (ancestral-descendant relation) through a differentiated analysis of the characteristics of a set of species including an ancestral (hypothetical) and all its descendant (Wiley & Libermann, 2011).

Causality is a recurring theme in the work of Willi Hennig. In his main work, *Systematics Phylogenetics* Hennig (1966) refers to causality in two ways: as a concept of "causal relationship" linked to the idea of "truth" and “proof ", for real relationships; and the “[k]nowledge of the causal processes involved in the form change of individuals and in changes in the fabric of the species belongs to a knowledge of the causal processes-the mechanism-of evolution.” (Hennig, 1966: 200), that is, the causal evolutionary processes resulting from the evolution from the descent with modification of the individuals. Although it is not linked to the idea of explanation, this Hennigian causality in its second meaning, has explanatory connotations because knowing which processes gave rise to differences between organisms is part of their causal understanding. This second connotation is reinforced in his great work on insect phylogeny (Hennig, 1981). In this paper, he reinforces that phylogenetics “[m]ust develop into evolutionary biology or ecology and become 'causal research ’” (Hennig, 1981: 38). To illustrate this point Hennig (1981: 42) gives us the following example: “It is possible to explain the holometaboly of the Holometabola by showing that a change has taken place in the hormonal system regulating metamorphosis, causing the corpora allata to release an inhibiting hormone… In one sense this is a 'causal explanation ' of the fact of complete metamorphosis during the ontogenetic development of a single individual. Yet it reveals nothing about the **reasons** for the origin holometaboly in the course of phylogeny, on the basis of its 'biological significance'...” (my emphasis).

Thus, this quote is very approximate to the model of explanation of biology made by Mayr[4] (1982) - the proximate causes of holometabolism, and the ultimate (evolutionary) hypothesis would be hypotheses about the effect of known evolutionary factors on what is known about the environment that probably existed at the time of the origin and development of the holometaboly, that would be of more relevance to systematics (Hennig, 1981). While aware of the inherent difficulty in tracing these causal events from far back evidences that was deteriorated millions of years ago (as it happens with other areas of the historical sciences), Hennig (1966; 1981) endorsed the need for broader explanations for systematics. One of the problems with Hennig's approach is its lack of operability. For example, only synapomorphies

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[4] Recently, some authors argued for the existence of some problems with the explanatory model of Mayr for Biology. Today, it is recognized that the proximate and ultimate distinction is in a reciprocally causal relation. This is the case, because, as Gardner (2017) argued, proximate explanation deal with mechanism, like ontogeny and molecular and embryological development, while ultimate explanation deals with the “adaptative rationale of this design”, or as I would put it, the functional explanation of a trait (that could be an adaptation). In this new way of thought, we can see the mutual interplay between these causal explanations that can lead to a fuller understanding of traits evolution and its possible adaptation.

could be explained causally? Would homoplasies have an explanation too? How to distinguish between well-confirmed and poorly-confirmed explanations? These topics remain virtually unexplored to this day.

2.2. Explanatory power, explanation and parsimony

“What is considered true or acceptable at a particular time is largely conditioned by historical causes. It may be nothing more than a matter of who wrote a textbook. In phylogenetics, traditions are among the most important characters, and all too often they are traditions masquerading as facts.”

Ghiselin (1997: 295)

Instead of following the path of Hennig (1966), systematists took other strategy and we shall see how the issues were dealt with in this discipline. Explanatory power, or the strength of an explanation, are conditions under which hypotheses are judged to provide strong versus weak explanations of some proposition (Schupbach & Sprenger, 2011). Thus, to have a better understanding of explanatory power one must have some clarity about what that thing is. In order to begin to examine how explanation and explanation power are considered in systematics, consider the following quotes: “The explanatory power of a genealogy is consequently measured by the degree to which it can avoid postulating homoplasies.” (Farris, 1983: 18)” And “The explanatory power of a genealogy is consequently diminished only when the hypothesis of kinship requires *ad hoc* hypotheses of homoplasy.” (Farris, 1983: 19). Thus, in Phylogenetics, the explanatory power talk are related to these quotations and to Farris. Taking his cue from Popper (1959), Farris (2008) even formalized a formula for explanatory power:

$$E(h,e,b) = \frac{p(e,hb) - p(e,b)}{p(e,hb) + p(e,b)}$$

Where *E* is the explanatory power of hypothesis *h* with respect to evidence *e*, given background knowledge *b*, that is, the power of h to explain e (given b) (Farris, 2008: 2). Thus, Farris (1983; 2008) created a symmetric relation between explanatory power and homoplasy: the higher the level of homoplasy, the lower the explanatory power; and by contrast, the lower level the homoplasy, the higher level the explanatory power. Farris's (1983) positions, in which he connects ideas about phylogenetic inference with more global questions about hypothesis evaluation, add that these "*ad hoc* hypotheses of homoplasy"[5], are not capable of explanation - including inheritance from a common ancestor - at all. When a genealogy, or better, a phylogenetic tree, provides us with a homology (apomorphy) hypothesis, Farris argue that we are able to provide an explanation for these shared derived traits, and this explanation is due to inheritance. This is so because: "*A genealogy is able to explain observed points of similarity among organisms just when it can account for them as identical by virtue of inheritance from a common ancestor*." Farris (1983: 18), while homoplasy cannot give this explanation, mainly because the explanation ("inheritance from a common ancestor") cannot be given, accordingly to Farris.

Therefore, the Farris's thesis about the asymmetry between homology and homoplasy, and in this way, is a corollary of his symmetry between explanatory power and homoplasy. However, if his asymmetric relation between homology and homoplasy does not hold, this explanatory power schema fails as well. This is exactly what Sober (1988) concluded, arguing that no genealogical hypothesis explains "by itself" any character distribution, whether homoplasy or homology. Then, Sober points to the fact that in no significant sense genealogical hypotheses are unable to explain the character distributions they imply to be homoplastic. The problem is that genealogical hypotheses may weakly explain homoplastic and homologous characters, both contributing to genealogical explanation. So with this conclusion, the scheme of explanatory power developed by Farris (1983) does not hold and it must be discarded. Another line of criticism is the one given by Vogt (2013) who argues, persuasively, that homoplasies are the result of evolution, being part of its background knowledge. Thus, it cannot be characterized as *ad hoc* hypotheses[1]. Therefore, thoroughly this essay I will deal with homoplasy in its appropriate form: as an explanation, not as an error. Besides, a homoplasy can group some taxa, the matter here is in relation to a hierarchal correlation of characters; some will give signal - synapomorphy - for some clades and others simple will not.

However, other cladists continued with this popperian asymmetry tactic. Thus, based on Farris' (1983) argument, Kluge (1999; 2001) formalized Hempel's model of explanation for the cladistics. Following this path, the following quote that Kluge (1999: 421) shows how he

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[5] When systematists avoid explanation instances in relation to homoplasy, and with that convergence, they are excluding from their analysis the natural selection of adaptations that came about in the form of homoplasies. Thus, groups can defined by non-adaptive or, more precisely, selectively neutral characters.

transforms the model: “Taking my cue from Popper (1957), I too will assume Darwin’s principles of “descent, with modification,” as the necessary explaining theories (L) in a deductive historical model of explanation, with cladogram, and its common ancestral relations, constituting the specific initial condition (C) and synapomorphy the specific event to be explained (E).” This formalized deductive scheme for application in cladistics elaborated by Kluge (1999) takes the following form:

L, descent, with modification
C, cladogram
______________________________ explanation
E, synapomorphy.

The “law” would be “descent with modification” and from it, we would make a deduction about synapomorphies; never homoplasies (Kluge, 2001) because they “don't explain anything” (as argued by Farris (2008). Thus, for Kluge (2009) a causal explanation can only be reached when proceeds from a known or given effect, or initial conditions - effect - to an unknown cause, assuming a theory or universal law.

Thus, these cladists used Popper in the same Deductive-Nomological model of Hempel's explanation that disregarded any mention of causal elements. Following this model, as it will be shown, the systematists disregarded causality, and instead adhered to a hypothetical-deductive approach to cladistic analysis (Gaffney 1979). A good example of this pattern is the following quote from Platnick (1982: 283), where he rejects causality as irrelevant to cladistic analysis: “*But one needs no causal theory to observe that of all the millions of species of organisms in the world, only about 35,000 of them have abdominal spinnerets… One needs no causal theory to observe that of the thousands of (cladistically treated) characters that have been found to vary among those 35,000 species, not a single one has been shown to be unique to only some of those 35,000 species plus any species outside of those 35,000*.” So the question of causation was decreed, and it was regarded as a no important or necessary for systematics. This is what Hempel (1965) demanded for a complete explanation in science and we already saw that this model does not work; and we shall see in details how this model of explanation - the nomological-deductive model - functions, his critics and if this is a valid mode in evolutionary biology, and by consequence, in systematics.

2.3. Beyond Popper: Abduction in Phylogenetic Systematics

We also have Fitzhugh's (2006) model using abductive logic to obtain scientific explanation with its respective understanding. Fitzhugh (2006: 39) is explicit in the need to create a causal explanation in systematics: "*In order to assert the explanatory nature of phylogenetic hypotheses, we must recognize that all explanatory hypotheses follow from specific causal questions*." However, Fitzhugh relies on the abductive logic in which there is the notion of explanations such as "self-evidence," where the phenomenon that is explained in turn provides an essential part of the reason for believing that the explanation is correct. Only when we ask how well various hypotheses would explain the available evidence, that we can determine which hypotheses merit acceptance (Lipton, 2001). The appropriateness, then, made by Fitzhugh (2006) regarding cladistics is when, using parsimony with abduction, refers to the relationship between causal questions and an explanatory hypothesis, with the application of an accepted causal theory to connect effects (character distribution) on the final relationship hypothesis that will provide an answer to a more parsimonious causal question.

Causal inferences have two types of use: inferential, to make predictions, confirmations, and explanatory use, to account for why an effect occurred. Alternatively, we need to make a clear distinction between two types of "why-questions", i.e., explanations of why and confirmation questions of why. These distinctions can be made as follows (Salmon, 2001: 79): "*Explanation-seeking why-questions solicit answers to questions about why something occurred, or why something is the case. Confirmation-seeking why-questions solicit answers to questions about why we believe that something occurred or something is the case*." If Fitzhugh's abduction is correct in its logic, we must conclude that it belongs to the theory of scientific confirmation, not to the theory of scientific explanation. Thus, to explain an event (or a series of character transformation), it is necessary to invoke some kind of theoretical knowledge (such as that discussed by Hennig [1981]) with the physical connections between facts and events and their binding mechanisms, between causes and effects (Salmon 1998). Another problem with abduction, is that when we have a number of potentially adequate explanations, like the possible explanation of a trait evolution - pleiotropy, natural selection, natural selection, so on (or some combined elements as well) - so, the argument to the best explanation is not valid when we have several possible explanations that are **equally** good (Sterenly & Griffiths, 1999).

From this, we can see the lack of a well-grounded theory of explanation in phylogenetic systematics. These problems remain persistent to this day because, as argued earlier, there has been an abandonment by the systematists an objective to optimize and operationalize cladistics as a causal science. Current theories suffer from problems that can only be circumvented with a model of explanation that takes into account the fundamental role of explanation and causalities in understanding phylogenetic relationships (whether synapomorphic or homoplastic). In order to present a potential solution, I will show and discuss the main theories of explanation and causality in the philosophy of science. This will give us the weapons to know which, if any, of these models could be used to be used to replace Hempel's and Popper's model of scientific explanation.

3. A primer on understanding, explanation and causation

3.1. Scientific Understanding: What it means to understand something?

It might seem a commonplace to say that the aim of science is to provide understanding of the world around us. Scientists and laypeople alike will typically regard understanding as one of the most important and highly-valued products of scientific research. In the past centuries scientific research has enormously increased our understanding of the world. As Salmon (1998) argued, it is widely agreed that one of the chief aims of scientific endeavor is to facilitate our understanding of the universe in which we live and of our place in it, with the scientific practice functioning as a bridge to accomplish such a goal. Thus, it seems a commonplace to state that the desire for understanding is a chief motivation for doing science. However, what do we mean when we say that scientists understand, for example, global climate change? What is involved in achieving scientific understanding of phenomena, be they the origin of the universe, the structure of matter, the behavior of organisms, or economic and social developments? (Regt *et. al.*, 2009).

We can affirm that the sciences gives us with **explanations** and therefore contribute to our **understanding** of nature and social behavior. However, since both words -"explanation" and "understanding" - are highly ambiguous (creating opportunities for obfuscation and confusion), it is essential to distinguish the variety of senses. Let us begin with "understanding" and turning our attention to "explanation," afterward. Salmon (1998) distinguish four major types of understanding: empathic; symbolic; goal-oriented and scientific understanding. The last one that will be the focus on this section and throughout this essay. Before that, we shall discuss, briefly, each one of these types:

Empathic understanding: “This natural tendency to share and understand the emotions and feelings of others in relation to oneself, whether one actually witnesses another person’s expression, perceived it from a photograph, read about it in a fictive novel, or imagined it, refers to the phenomenological experience of empathy” (Decety & Meyer, 2008: 1053). Thereby, in many contexts, understanding refers to empathic sharing of feelings; to understand another person's behavior is to know that person's motives, values, desires, and beliefs.

Symbolic understanding: A certain type of understanding relates directly to language; it emphasizes communication and meanings. An outstanding example of revelation of meaning is the deciphering of the Rosetta Stone, discovered in July 1799 at Rosetta (now el-Rashid) in Egypt's north-west Delta, and part of the British Museums collections since 1802. The Stone, a fragmentary granite stela inscribed with a bilingual text in ancient Egyptian and Greek, played a crucial role in the eventual decipherment and understanding of Egypt’s hieroglyphic script (Parkinson, 1999). Archaeologists interpret symbols and it serves primarily as instruments of communication, and many powerful symbols in any culture are the commonest things: bread, water, houses, the river, and the hills beyond. Powerful symbols are not irrational and ethereal but are often highly rationalized and concrete: Money is a symbol rather than mere gold, paper, or numbers in an account (Robb, 1998).

Goal-oriented understanding or teleological thinking: teleology with be dealt with much details in chapter 8; in this section, a brief overview will be discussed. We can achieve a different kind of understanding by invoking purposes, aims, or goals. This type of understanding splits into two sub-types corresponding to two types of explanation. First, human behavior can often be explained in terms of conscious motives and purposes. For example, I carry water on a desert hike because I expect to be thirsty, and no drinking water will be otherwise available. This is, of course, a teleological explanation. The familiarity of such explanations makes them seem especially appropriate when understanding is required. We readily extend such explanations to the behavior of other humans. This kind of understanding tends to blend into empathic understanding, for knowledge of the desires and values of others enables us to know, if not share, their feelings. In the second subtype functional explanations provide understanding. We understand why our blood contains hemoglobin: its function is to transport oxygen from the lungs to other parts of the body, where it is needed for the metabolic processes that sustain the life of the organism. This is a subtype of the scientific understanding that Salmon, Hempel and other philosophers mean by “scientific”. With the objective to disparage the understanding of meanings (to avoid confusion between explanations of meanings and explanations of events and phenomena) Salmon (1998), gives emphasis that we come to understand a meaning when we can say what something means; and that we come to understand a phenomenon when we can explain why it occurred.

Where human behavior and teleology in biology is concerned, an appeal to purposes often provides a suitable explanation. The term “teleological” derives from the Greek word telos, meaning “goal” or “end.” Hence function ascriptions are often thought to be a type of teleological explanation (Garson, 2008). As an example of teleology in biology, we can use evolutionary biology. Thus, features of organisms that may be said to be teleological are those that can be identified as adaptations, whether they are structures like a wing or a hand, or organs like a heart or a kidney, or behaviors like a wolf hunting a rabbit or the courtship displays of a peacock. These examples are a consequence of natural selection, because their existence is ultimately accounted for in terms of their contribution to the reproductive fitness of the organisms (Ayala, 2016). They present a legitimate understanding mainly because do not require appeal to any extrascientific agency (Salmon, 1998).

Scientific understanding: The fourth major type of understanding is linked to **scientific explanations** in the physical, biological, behavioral, and social sciences. Its cognitive dimension is primary. Scientific explanations must be based on well-established scientific theory and fact; psychological comfort is not at issue. This point deserves emphasis.

Therefore, it is not merely incidental that explanation may provide understanding; rather, it provides understanding is the inherent function of explanation (Faye, 2014). So, why do we ask scientists to produce explanations? What is explanation used for in science? What is its purpose? Now, we known that an obvious reply is that we seek explanation because it provides information and imparts understanding. Successful explanations are attractive because they provide us with an understanding of what they are supposed to explain. Today, although the consensus that explanations are explanatory because they yield understanding is growing, views about understanding remain divergent for some authors[6] (Faye, 2014). So, we can say that the correctness of explanation is a necessary condition for scientific understanding, but that is not a sufficient condition; as cognitive factors, a subject matter, and research group objectives are relevant as well. However, I argue for the essential epistemic and ontological

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[6] For instance, Regt *et al* (2009), argued for the pragmatic aspects of understanding. They emphasis the relation involving a subject. The purpose and effects of scientific understating for the particular persons who use and applies understanding as the end-product of explanatory activity (the cognitive state achieved, the goal of explanation), because it is the state of a cognizing subject. Therefore, gaining understanding through explanations is not an automatic process, but rather a cognitive achievement in its own right.

importance of explanation in understanding. Obviously in science as in everyday life, we pursue explanation because it provides us with understanding. The fact that understanding comes with explanation is not a contingent feature of explanation but is the purpose of making explanations. Finally, concerning scientific explanation, I hold that neither does knowledge imply understanding, nor does understanding imply knowledge. They are closely, but not logically, connected. They are closely connected because we can have knowledge without understanding, but we can't have understanding without knowledge. Each of us knows many things that we don't understand because we cannot explain why they are as they are.

Take the following example, which is a modification of Faye (2014): you enter a hotel room and want to watch TV. You try to switch it on by the remote control, but nothing happens. You look around in an attempt to solve the problem, and you realize that the TV is unplugged. The moment you see this, you seem to known why the TV does not work. As part of your background beliefs and assumptions you know that a TV needs electricity. So when you connect this information with the piece of information about the unplugged TV, you feel certain why it doesn't work properly, namely in virtue of being disconnected from the electric circuit. In this situation it seems that you have a good knowledge of the problem. Now, assume that you then plug in the TV, but that it still fails to work. Again, you become puzzled because your knowledge of the problem up to then was not equivalent to understanding. You then call the receptionist who tells you that the TV in your room broke down this morning, and then she calls the repairman to fix it. When the repairman arrives, you tell him that you know that the TV doesn't work, but you don't understand why. He then begins to check the TV and realizes that the problem was with the electron gun circuit (that part the signal into separate red, blue, and green signals to drive the image to the monitor). When in possession of this new information, you now **understand** why the TV was not working, in addition to just **know** that the TV doesn't turn on. Now, the TV can be appropriately fixed it. Thus, we can possess knowledge without having factual understanding. We will comeback with this notion later, but for now we can say that to understand something, within the context of scientific explanation, is to have a deeper and more holistic conception (we can say that we can open the black-box) of a phenomenon than the description of its superficial characteristics.

3.2. Explanation: What is an explanation?

It is well known that science seeks explanations to satisfy our wonder to understand the world we live in. Etymologically, the word explanation is derived from the Latin *explanare*, meaning to make plain. Beyond that, the term has been used in a wide variety of ways in our language—we speak of explaining the meaning of a word, explaining the background to philosophical theories of explanation, explaining how to bake a pie, explaining why one made a certain decision (where this is to offer a justification) and so on. So, if scientific understanding is achieved by explanation, it is important to make some clarifications, mainly disambiguation; what types are there, and how a scientific explanation is structured. Let us begin by the differentiations, once again, made by Salmon (1998: 5): explanation of meaning, who-questions:

“People often ask for explanations of *meaning*—whether of an ordinary word, a poem, a painting, or another work of art. The meaning of a word may be found in a dictionary. The meaning of a poem may be clarified by calling attention to certain metaphors. The meaning of a painting may be exhibited by reference to the iconography of the period in which the work was created. If the process has been successful, we have achieved understanding of the word, the poem, or the painting.

Another type of explanation involves learning *how to perform* certain activities. A painter might explain how to achieve an appearance of depth by the use of perspective. An automobile owner's manual might explain how to jack up the car in order to change a tire. A guidebook for tourists might explain how to find a particular building in a foreign city.”

Thus, Salmon distinguishes explanations of meanings and “*what something means* or *how to do something”* (Salmon, 1998: 5). In explaining the rules of succession in an Egyptian dynasty, or the symbolism of a tribal dance we can see that they are clearly a different kind of explanation, the explanation of meaning, not at all related to scientific explanation (Scriven, 1962). Besides examples made by everyday activities by the layperson, explanations of how to perform various activities are also found in science; a scientist might explain to a student, for instance, how to follow determinate protocol to extract a DNA sample. However, when we speak of scientific explanation, we are not usually referring to these kinds of explanations. Mainly, we want to explain **why** determined phenomena occurred. For example, the hypothesis that contemporary life on earth descends from a last universal common ancestor (Cleland, 2009). All life on earth today contains, in their hereditary material (nucleic acids), remarkable molecular similarities. The best explanation for these extraordinary similarities in molecular composition is not that they represent a fantastic coincidence but that all life on earth today inherited them from a last universal common ancestor. Although the historical explanation is a complex matter, it is still about a particular event and not a general regularity.

Salmon (1998) argues that these explanations could be made using why-questions: “Why did the organisms share extraordinary similarities in molecular composition?” This is how we obtain scientific explanation. However, before we proceed on clarification on how do we explain why-question on scientific explanation, we need to mention that **not all why-questions are requests how questions for scientific explanations**. For instance, Braillard & Malaterre (2015) discussed two cases where an explanation are not causal ones: the first is the equilibrium explanations for the Fisher’s explanation of sex-ratio equilibria of Sober (1983); and a number of mathematical explanations in biology and in science in general.

3.3. Causation: What is causation?

As it happens to natural science, to explain in the social sciences is, in various cases, a causal matter (Elster, 2015). Salmon (1998), in this line, without insisting that all scientific explanations are causal, argues that we can still maintain that knowledge of causal relations enables us to explain a vast range of natural phenomena, and that such explanations yield understanding of the world. Causal concepts are in every branch of science and in everyday life-making decisions regarding ourselves, and other living persons. So, in order to make the “cause” as precisely as one can, it would be useful to, one more time, discriminate the various meanings of the word “cause” (Salmon 1988: 4):

“Causal concepts are central to our *practical deliberations*. We need to know the causes and effects of depletion of ozone in the upper atmosphere. We need to know whether “secondhand” smoke causes harm to human health.”

“*Everyday practical planning* involves causal considerations. We avoid leaving iron tools out in the rain because exposure to moisture causes them to rust. We plant seeds in springtime in order to reap food or flowers later on.”

“Causal terminology permeates *ordinary language*. Note how many common verbs express causal efficacy: “break,” “fix,” “move,” “send,” “hurt,” “help,” “make,” “antagonize,” “comfort,” etc.”

Philosophical investigations of causality have a long history and broad relevance. As the preceding paragraph shows, causality figures prominently in ethics; for similar reasons it is present in legal, social, and political philosophy (Salmon, 1998). In everyday situations, just as it happens in science, usually we want to explain a singular fact or event. For instance, the extinction of the dinosaurs. The most natural way to explicate what is called for when such an explanation is proposed, is to say that an explanation is needed when we know that E, the effect has happened, but we lack knowledge of *C*, its cause. Thus to explain why the dinosaurs were extinct at the end of the Cretaceous period (the effect), we need to use, with the most supported hypotheses, that it was due to an extraterrestrial impact, such as an asteroid (the cause). Knowing causal processes operating in experimental or historical scenario is a precondition of successful experimentation (or recollecting past pieces of evidence for a search for a common cause) and explanation, as long as there exists a relation between facts, events, or phenomena that obeys the criteria necessary for applying the embodied notion of causation. But what are these criteria? How do we know that we are dealing with cause-effect condition and a not a merely a correlation matter?

Before we go any longer in the relation between scientific explanation and causality it is worth noting, however, that in all of these discussions, unless we engage in preliminary clarification of the concept we are attempting to explicate, in our case, *scientific explanation and causality*, we may miss the very concept we are trying to explicate (Salmon, 1989). The clearest expression of that goal was given by Rudolf Carnap (1962); thus, in Carnap's words (1962: 3): "By the procedure of explication we mean the transformation of an inexact, prescientific concept, the *explicandum*, into a new exact concept, the *explicatum*." So, when we ask 'What is causality?', 'What is scientific explanation?', etc., which are frequently used by scientists and by others who talk about science, is vague and, possibly, ambiguous we often immediately start to look for an answer without first examining the tacit assumption that the terms of the question are at least practically clear enough to serve as a basis for an investigation. Carnap (1962: 6) gave the following example to illustrate these differences: "Let us consider as an example the prescientific term 'fish'. In the construction of a systematic language of zoology, the concept Fish designated by this term has been replaced by a scientific concept designated by the same term 'fish'; let us use for the latter concept the term '*piscis'* in order to avoid confusion. When we compare the *explicandum* Fish with the *explicatum Piscis*, we see that they do not even approximately coincide. The latter is much narrower than the former; many kinds of animals which were subsumed under the concept Fish, for instance, whales and seals, are excluded from the concept *Piscis*." Thus, in order to give a full articulation of explanation and causality requires an adequate characterization of scientific explanation.

To sum up, we reached the conclusion that **understanding** is achieved when we, say, investigate the mechanism of an old-fashioned mechanical watch, seeing how each part functions in relation to the **explanation** all the other parts. The ability to provide a **causal** description of how the springs and gears work constitutes our understanding of this phenomenon. In the next section, we shall see how various philosophers have formed different characterizations of an explanation, the various theses about causality, and how systematists used these concepts.

4. Classic views on Scientific Explanation

4.1. Brief history: from Greece to the "received view"

This section is for the purpose of contextualization only and is principally based on the works of Psillos (2007) - for explanation - and Losee (2011) - for causality. We refer the reader to those authores for a more detailed account on the history of explanation. We shall begin by looking at the Greek noun, *aitia* and its cognate adjective *aitios, aition*; *aitia* is traditionally translated as 'cause', although many prefer 'reason' or 'explanation' (Broadie, 2010). As in various topics in philosophy, we start our brief and selective historic journey with Aristotle. His his conception can be briefly stated as the thought that explanation consists in finding out why something happened and that answering why-questions requires finding causes, and it set the agenda for almost all subsequent thinking about explanation thought history (Psillos, 2007). He stressed the interdependence of causal analysis and scientific explanation, holding that scientific explanation is achieved when there is a gain in knowledge from knowledge of a fact thought a knowledge of the reason why the fact is the way it is. Aristotle required a fact to be expressed as the conclusion of a sound deductive argument whose premises state the cause of the attribution made in the conclusion (Losee, 2011).

According to Aristotle, following Losee (2011), there are four aspects of such arguments:

1. the form of the process (*formal* cause),

2. the matter transformed (*material* cause),

3. the interaction between the transforming agent and that which is transformed (*efficient* cause), and

4. the *telos*, or purpose, of the process (*final* cause).

The **material cause** of a statue is its material (e.g., bronze); its **formal cause** is its form or shape; its **efficient cause** is its maker; and its **final cause** is the purpose for which the statue was made (Psillos 2007). These different types of a cause correspond to different answers to why-questions. Being an empiricist of his time, Aristotle thought that knowledge of causes has experience as its source. But experience on its own cannot lead, through induction, to the first principles: these are universal and necessary and state the ultimate causes (Psillos, 2007). Unfortunately, one of the problems with his system (as this problem persist to nowadays) is that he was unable to stipulate a criterion to distinguish causal correlations from accidental correlations. He would insist that causal correlations must be true in each member of the subject class and the predicate term must be "essential" as a member of the subject class (Loseem, 2011).

Francis Bacon (1561–1626) led the attack against Aristotle's concept of "final cause" in the sixteenth century. He criticized mainly the final causes, or *telos*, and maintained that this notion is an especially pernicious predisposition; emphasized that progress in science depends on setting aside such concepts (Losee, 2011). As Bacon, René Descartes (1596–1650) criticized the notion of final causes; insisting that they are unscientific, a throwback to an earlier age of superstition. Thereby, Psillos (2007: 102) writes: "…he thought that the explanation of natural phenomena proceeds by means of mechanical interactions, and not by reference to violent and natural motions; nor in teleological terms." He diverged from Aristotle by two forms: the first is that the basic principles are the fundamental rules or laws of nature. The second was the idea that all explanations of natural phenomena are mechanical. Like Aristotle, Descartes thought that explanation amounts to the search of causes, but unlike Aristotle, he thought that all causation is efficient causation and, in particular, mechanical.

Descartes's conviction that the cause of motion is always the impact or pressure exerted by a contiguous body (or bodies) was widely shared. However, there are some motions that appear to take place without the benefit of impact or pressure. Important examples are magnetic attraction and the motions of the planets (Losee 2011). Cartesian causal explanation is, as we will see in Hempel (1965), nomological explanation (to find nomologically sufficient causes of the effects). Thus, causal explanations are demonstrative arguments whose premises include reference to laws of nature (Psillos, 2007). Hence the hypothesis must be consistent with the general laws of nature and with statements about relevant conditions, must be present for the statement about the phenomenon in question (Losee, 2011).

As we have seen, philosophers have been thinking about causation since at least 2500 BCE. And they linked explanation with causality, as we find in today's philosophy of science. However, ever since the devastating critics of the Scottish Philosopher David Hume (1711-1776), this concept changed for the better or for the worst, and it was where the modern discussions started (towards the epistemology or methodology of causal explanation). We will take special analysis of Hume because of his importance to the philosophy of causality, explanation and induction. First, it is important to state the reasons why Hume began his investigation. The philosophical, scientific, and theological controversies of the Enlightenment influence the arguments in every section of his 1748 book, *An Enquiry concerning Human Understanding*. Hume lived in an epoch know as `Enlightenment' that now refers to some principal European intellectual and cultural currents in and around the eighteenth century; it was used at the time by writers convinced that centuries of darkness and confusion were giving way to enlightenment in many fields of learning. Many philosophers began to search for a scientific framework that would correct excessive speculation in philosophy and eliminate guesswork. They also opposed intolerance and dogmatism in religion. Hume vigorously supported a scientific philosophy and denounced many aspects of traditional philosophy and organized religion, especially the zealous and the doctrinaire. Thus, Hume focused on causation and aimed to dissolve the issue of its metaphysical nature. Finally, the following quote resumes his motivations: “I shall venture to affirm, as a general proposition, which admits of no exception, that the knowledge of this relation is not, in any instance, attained by reasonings a *priori*; but arises entirely from experience, when we find, that any particular objects are constantly conjoined with each other.” (Hume, 1748/1999: 109).

Consider this line of reasoning (Losee, 2011):

If a figure is a triangle, then the figure has three sides.

This figure is a triangle.

Therefore, this figure has three sides.

This argument has one intuitively certain premises and one indisputable premise, and the conclusion follows logically. The premises entail the conclusion, *a priori*. Hume claims that causal reasoning is not like this model of demonstrative reasoning, even if their structures are superficially similar. Effects are not entailed by causes, and causal relations are known only by experience. Hence, Hume (1748/1999: 110) reasons that "…*causes and effects are discoverable, not by reason, but by experience*…"; following it, he gave the famous billiard-ball example: "When I see, for instance, a billiard-ball moving in a straight line towards another; even suppose motion in the second ball should by accident be suggested to me, as the result of their contact or impulse; may I not conceive, that a hundred different events might as well follow from that cause? May not both these balls remain at absolute rest? May not the first ball return in a straight line, or leap off from the second in any line or direction? All these suppositions are consistent and conceivable. Why then should we give the preference to one, which is no more consistent or conceivable than the rest? All our reasonings *a priori* will never be able to show us any foundation for this preference (Hume, 1748/1999: 112)."

As a rationalist guided by the experience, he developed, according to the traditional interpretation of Hume, what is known as a **Regularity Theory of Causation** (RTC). Experience, according to Hume, tells us that a cause is temporally prior and spatially contiguous to its effect, and that event would be similar to the cause that is constantly conjoined to the event similar to the effect. Our idea of causation is therefore a relation involving only a (a) temporal priority, (b) spatial contiguity, and (c) constant conjunction. The argument goes as follows: "The first time a man saw the communication of motion by impulse, as by the shock of two billiard-balls, he could not pronounce that the one event was *connected*; but only that it was *conjoined* with the other. After he has observed several instances of this nature, he then pronounces them to be *connected*. What alteration has happened to give rise to this new idea of *connexion*? Nothing but that he now *feels* these events to be *connected* in his imagination, and can readily foretell the existence of one from the appearance of the other" (Hume, 1748/1999: 145)"

Hence, for Hume, all we have is the habitus, that tells that we need to make a necessary connection between constative conjunction. In Hume words (Hume, 1748/1999: 123): "All belief of matter of fact or real existence is derived merely from some object, present to the memory or senses, and a customary conjunction between that and some other object. Or in other words; having found, in many instances, that any two kinds of objects, flame and heat, snow and cold, have always been conjoined together; if flame or snow be presented anew to the senses, the mind is carried by custom to expect heat or cold, and to *believe*, that such a quality does exist, and will discover itself upon a nearer approach."

In conclusion, the following arguments are pivotal to the rationalist beliefs that Hume rejects (Loose, 2011):

1. Causes contain their effects.

2. Causes entail their effects, just as premises entail conclusions.

3. Causes entail their effects because there is a necessary connection between them.

He argues that inductive reasoning is a causal or factual inference (because he never used the word induction), and it is not a product of reason and, for this reason, cannot provide demonstrations. How does experience of past events warrant or provide a foundation for beliefs about similar future events? Hume notes that we commonly rely on the principle that future events will resemble past events of the same type. It is important to give the full citation of this argument, because this will form, latter, what many philosophers (Popper mainly), called **the problem of induction**:

"When a man says, *I have found, in all past instances, such sensible qualities conjoined with such secret powers*: And when he says, *similar sensible qualities will always be conjoined with similar secret powers;* he is not guilty of a tautology, nor are these propositions in any respect the same.

For all inferences from experience suppose, as their foundation, that the future will resemble the past, and that similar powers will be conjoined with similar sensible qualities. If there be any suspicion, that the course of nature may change, and that the past may be no rule for the future, all experience becomes useless, and can give rise to no inference or conclusion. It is impossible, therefore, that any arguments from experience can prover this resemblance of the past to the future; since all these arguments are founded on the supposition of that resemblance." (Hume, 1748/1999: 117)

A regularity that has held in the past will or must continue to hold in the future will be circular and question-begging. This is called the **principle of uniformity of nature**. Hume's position on causal relation is extremely complex. He assigned four distinct meanings to the phrase "causal relation." (Loose, 2011). Hume maintained that a "genuine causal relation" fulfills four conditions: spatial contiguity, temporal succession, constant conjunction, and necessary connection. But there can be no knowledge of "causal relation" in this sense. So, Hume defines cause in the following two forms (Hume, 1748/1999: 146) "… we may define a cause to be *an object, followed by another, and where all the objects, similar to the first, are* *followed by objects similar to the second*. Or in other words, *where, if the first object had not been, the second never had existed*. The appearance of a cause always conveys the mind, by a customary transition, to the idea of the effect. Of this also we have experience. We may, therefore, suitably to this experience, form another definition of *cause*; and call it, *an object followed by another, and whose appearance always conveys the thought to that other*."

We have no sensory impression of a necessary connectedness between events, and it is not possible to deduce the existence of an effect from knowledge of its cause. Since "genuine causal relations" are necessarily connected constant sequential conjunctions, we can have no "genuine" causal knowledge. Moreover, knowledge that the members of two classes of events have been conjoined fails to provide a rational justification for projection onto instances not yet encountered (Loose, 2011). One of the main contributions that Hume offered to the following generations is that he defines 'cause' in terms of 'time,' presuming an already-established temporal order. This is what Dowe (2000) called the temporal theory of causal direction; that entails that the causal relation is asymmetric (That is, if A causes B, then it is not the case that B causes A). The advantage of incorporating a temporal theory is the possibility to provide a ready-made explanation of causal asymmetry to recognize a cause from effect (Dowe 2000). Finally, the fact of the uncertainty of future events, lead Hume to propose that confirmations are relatives (for a new reformulation o this problem, see Popper, 1959) (Hume 1748/1999: 115): "If we be, therefore, engaged by arguments to put trust in past experience, and make it the standard of our future judgment, these arguments must be probable only…"

The regularity view is clearly inadequate, however. Hume's "official position" fails as a theory of causal relatedness, because it is false that every *de facto* constant sequential conjunction is a causal relation (Loose, 2011). John Stuart Mill noted that the sequence day–night is a constant sequential conjunction of events, but that day is not the cause of night (nor vice versa). According to Mill, both day and night are effects of a further cause - a set of conditions that include the axial rotation of the earth, its relative rates of rotation and revolution, and the energy production of the sun. It also is false that every causal relation is a *de facto* constant sequential conjunction. See the following practical example: Bob's exposure to a burst of radiation caused his death even though only 10 percent of healthy individuals at the same distance from the source died as a result of their exposure. The regularity view, which requires that every event *c* be followed by an event *e*, cannot account for the causal significance of Bob's exposure. Since we assign causal significance to numerous statistical correlations that are excluded by the regularity view, the regularity view is not a necessary condition of causal relatedness (Loose, 2011).

In his monumental *System of Logic* (1843), Mill defended the Regularity View of Causation. He insisted that regularities are necessary for causation, and added the sophisticated addition that for an effect invariably follow from the cause, this cause should not be taken to be a single factor, but rather whole conjunction of conditions that are sufficient and necessary for the effect to be manifested (Psillos, 2007). Mill argued that regular association is not sufficient for causation; there are regularities that are not causal and do not constitute laws (Psillos, 2007), and consequently, whatever we identify the cause of a given effect, it will, in fact, only ever be **part** of the cause. For instance, we might say that the short circuit caused the fire, but the short circuit was only caused by the fire because of the presence of flammable material and the absence of a sprinkler. There is no exceptionless regularity relating short-circuits and fires. What Mill perceived was that there could be no adequate characterization of the distinction between laws of nature and merely accidentally true generalizations, unless we adopted a holistic view of the lawhood.

Mill was a committed inductivist, who took all knowledge to arise from experience through induction. With Hume, he denied that there could be any certain and necessary knowledge. He should also be credited with the first attempt to articulate the Deductive-Nomological model of explanation, which became prominent in the twentieth century (Psillos, 2007). However, that didn’t guarantee that these methods were accused of some basic problems. As Psillos (2007: 121) argued: “Mill, however, was adamant that his methods (and the scientific method in general) work only if certain metaphysical assumptions are already in place. It must be the case that: a) events have causes; b) events have a limited number of possible causes; c) same causes have same effects, and conversely; and d) the presence or absence of causes makes a difference to the presence or absence of their effects.”

Ascribing for 20th century debates of causality, Bertrand Russell, in an influential essay (Russell, 1913), issued a challenge to theorists of causality: “…the word ‘cause’ is so inextricably bound up with misleading associations as to make its complete extrusion from the philosophical vocabulary desirable ...

> All philosophers, of every school, imagine that causation is one of the fundamental axioms or postulates of science, yet, oddly enough, in advanced sciences such as gravitational astronomy, the word ‘cause’ never appears. Dr

> James Ward ... makes this a ground of complaint against physics ...To me, it seems that ... the reason why physics has ceased to look for causes is that, in fact, there are no such things. The law of causality, I believe, like much that passes muster among philosophers, is a relic of a bygone age, surviving, like the monarchy, only because it is erroneously supposed to do no harm." (Russell 1913: 1)

Most philosophers have rejected Russell's main conclusion (mostly for good reasons), but Hitchcock (2007) brought to discussion what Russell got right. Russell seems to make the following claims:

r1 The notion of cause is incoherent, or fundamentally confused.

r2 The word 'cause' has 'misleading associations', and should be eliminated from philosophical usage.

r3 There are no causes.

r4 The 'law of causality' is obsolete and misleading.

Hitchcock (2007) considered r4 as basically correct, and argued that r1 is fundamentally mistaken. While claim r2 survives in a much modified form. About the r4 Russell, while declaring as false, wrote that: "We found first that the law of causality, as usually stated by philosophers, is false, and is not employed in science. We then considered the nature of scientific laws, and found that, instead of stating that one event A is always followed by another event B, they stated functional relations between certain events at certain times ...We were unable to find any a *priori* category involved: the existence of scientific laws appeared as a purely empirical fact..." (Russell, 1913: 26)

Hence, the rejection of the law of causality is definitely something that Russell got right (Hitchcock, 2007). While rejecting r1, Hitchcock (2007) argues that the problem with the notion of cause resulted in part from its combination of two distinct elements: cause and effect are supposed to stand in a relation of temporal contiguity, and also of invariable association. Thus Russell raises the possibility that our notion of cause may be incoherent because it attempts to combine incompatible elements. Indeed, our notion of cause seems to involve (at least) two different dimensions: cause and effect *covary* in some way; and they stand in certain kinds of spatiotemporal relations to one another. And finally, about r2, Hitchcock (2007) modifies the claim of Russell (1913: 1) that "the word 'cause' is so inextricably bound up with misleading associations as to make its complete extrusion from the philosophical vocabulary desirable", arguing that as there are many types of causal relationship, what is needed is not so much the elimination of the word 'cause', but to the introduction of more precise terms for characterizing causal concepts.

If one could conclude anything from this brief history is that before Hume's classic landmark criticism of causation (1748), the relation between cause and effect regarding explanation was not disputed. The concept of causality (as a necessary consequence, explanation) has been philosophically suspect ever since Hume's critics. Russell's position in condemnation of causality is a common position in philosophers with an empiricist tradition, mainly in the early years of the 20th century. An explicit definition of the notion of a scientific explanation that could serve for making this concept coherent, fundamentally precise and with clear associations (in opposition of Russell's criticism) had to wait two thousand years, with the publication of Hempel and Oppenheim's (1965 [1948]) work, *Studies in the Logic of Explanation*. They completed the demand that philosophical analysis must result in a precise and complete definition, in part because of a reflection of the influence of mathematical logic on the Logical Positivists and their immediate successors in the philosophy of science, like Hempel[7]. The advantage of such definitions is clarity: there will be no borderline cases and no unresolvable arguments about whether some proposed explanation is "scientific" or not. Before ending this brief historical section, it is very important to note that biology and all of its elements were set aside from the discussions about causality. Likewise, this trend is followed until the earlier to mid 20th century.

4.2. Hempel and the Received View

Salmon's *Four Decades of Scientific Explanation* (1989) is an excellent historical narrative about the nature of scientific explanation that occurred during the period between 1948 to 1987. Although Salmon begins his story in 1948 with the publication of "Studies in the Logic of Explanation," by Hempel and Oppenheim, we must be clear that these matters did not began in this date. The first philosopher to propose a model for scientific explanation was

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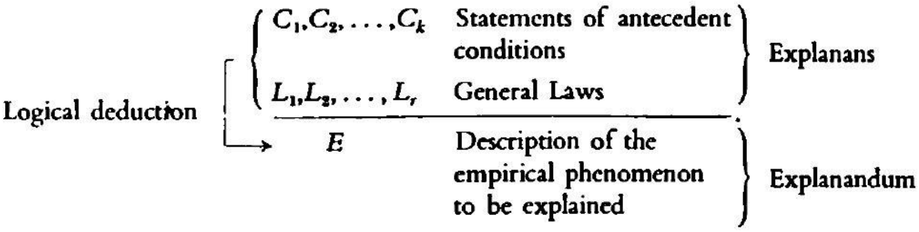
[7] However, even though Hempel and Oppenheim identify some explanations as causal explanation with D-N model (1965 [1948]), their official explication makes no reference to any causal requirements. In "Aspects," Hempel explicitly rejects the idea that causality plays any essential explanatory role (1965). It was only with the publication of Salmon's (1984) *Scientific Explanation and the Causal Structure of the Word* that causation became central in many explanatory accounts.

Karl Popper in his *Logik der Forschung* (1935), which was reissued subsequently to an English edition, *The Logic of Scientific Discovery* (1959). However, as Salmon (1984) argues, because his analysis was not as precise as the work of Hempel and Oppenheim, and Popper's work and influence increased dramatically only when he launched his English translation, he chooses the 1948 as the date of the modern analysis of explanation[8].

Thus, according to the account made by Hempel and Oppenheim (1948 [1965]) a Deductive-Nomological explanation (hereafter D-N explanation) of a particular event is a valid deductive argument whose conclusion states that the event to be explained did occur; the root of the term '*nomological'* is the Greek word '*nomos'*, for law. This conclusion is known as the *explanandum*-statement. Its premises, known collectively as the *explanans*, must include a statement of at least one general law that is essential to the validity of the argument, that is, if that premise were deleted and no other change were made in the argument, it would no longer be valid. The logical structure are defined as follows (Hempel and Oppenheim 1965 [1948]: 246): "[t]he explanans falls into two subclasses; one of these contains certain sentences C1, C2, ..., Ck which state specific antecedent conditions; the other is a set of sentences L1, L2, .., Lr which represent general laws." They gave the following schema to characterize a scientific explanation:



The explanation is said to subsume the fact to be explained under these laws; hence, it is often called "the covering law model."; thus in Hempel and Oppenheim words (1948 [1965]: 246) "[T]he event under discussion is explained by subsuming it under general laws, i.e., by showing that it occurred in accordance with those laws, in virtue of the realization of certain specified antecedent conditions." An argument fulfilling the foregoing conditions qualifies as a **potential explanation**. If, in addition, the statements constituting the explanans are true, the argument qualifies as a **true explanation** or simply an explanation (of the D-N type). Thus, an

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[8] There are some authors that considering their similarities, call this model a "Hempel and Popper" model of explanation (Caponi, 2014).

explanation can be described as *an argument to the effect that the event to be explained was to be expected by virtue of certain explanatory facts* (Salmon 1989).

The general conditions of adequacy, which were summarized by Salmon (1989), are divided into two groups, logical and empirical. Among the logical conditions we find:

(1) the explanation must be a valid deductive argument,

(2) the explanans must contain essentially at least one general law,

(3) the explanans must have empirical content (it must be testable).

The only empirical condition is:

(4) the sentences constituting the explanans must be true (not just highly confirmed).

Thus, a potential explanation fulfils only the logical conditions, whereas a true explanation must additionally meet the empirical condition (Faye, 2014). As an example of 'the covering-law model of explanation,' we can give an example concerning the conducting of electricity by a piece of cooper. So we create a particular event, "Cooper is a metal", and to explicit a general law, in this case "All metals conducts electricity". Thus, we have distinguished the *explanans* (the law and the particular event) which is to be explained, and the *explanandum* (the fact that cooper conducts electricity). With these statements we can build a logical deduction of the explanation: from the premises "All metals conducts electricity" and "Cooper is a metal" we can deductively derive the conclusion "Cooper conducts electricity", that is how we explain something bringing it under a covering law. Thus, the foregoing explanation is to be viewed as a deductive argument. It can be set out more formally as follows:

Why does copper conduct electricity?

$$\left.\begin{array}{l}\text{All metals conduct electricity. (Law)}\\ \underline{\text{Copper is a metal. (Initial conditions)}}\end{array}\right\}\quad\text{Explanans}$$

∴ Copper conducts electricity Explanandum

It is important to note that the single line separating the premises from the conclusion signifies that the argument is deductively valid. Thus, the first two statements constitute the explanans, in which we find both empirical content (initial conditions) and general laws, all of which are true in this case. The final statement, which is the explanandum event to be explained, follows logically from the explanans, and therefore all four criteria are met. The logical validity of the argument lends it both explanatory and predictive power.

4.3. Famous Counterexamples and some general problems with the D-N model

This model gave rise to much criticism. One type of criticism was in relation to the symbolic logic and artificial language developed by Hempen and Oppenheim (as was the case with every participant of the "logical empiricism" movement). I will not discuss these issues here (but, see Salmon, 1989). One of the most important reasons it fails is that it proposes such a narrow definition of explanation - so narrow that it unproblematically applies to only a part of physics (Faye, 2014). So, the Deductive-Nomological model of explanation seems to be useful only in those cases where we can consider the explanandum-event as being part of a very isolated, well defined, and idealized situation. Thus the widely accepted deductive nomological model of scientific explanation that sprung from Hempel and Oppenheim's original thesis has met with important challenges.

Salmon (1989) gave seven counterexamples against the Deductive-Nomological Model of scientific explanation by Hempel. These examples fall into two broad categories: (1) arguments that fulfill all of the requirements for D-N explanation, yet patently fail to qualify as bona fide explanations - they show that the requirements set forth by Hempel and Oppenheim are not *sufficient* to determine what constitutes an acceptable scientific explanation. We shall contemplate, briefly, the following examples: Bromberger's flagpole example (1), the barometer case (2) and the case of the birth-control pills (3) are of this form - and (2) examples of allegedly bona fide explanations that fail to fulfill the Hempel-Oppenheim requirements; they are meant to show that it is not *necessary* to fulfill those requirements in order to have correct explanations. The ink stain example (4) is of this last one. Finally, we shall see the problems of this model in relation to the laws and the "symmetry thesis".

> (1) If we know the elevation of the sun in the sky and the height of a flagpole, we can compute the length of the shadow of the flagpole; or if we know the length of the shadow, we can compute the height of the flagpole. This deduction may be accepted as a legitimate D-N explanation of the length of the shadow. However, only the presence and height of the flagpole explains the occurrence and length of the shadow but not the other way round. It is because "a causal process is involved, and that the light from the sun must either pass or be blocked by the flagpole before it reaches the ground where

the shadow is cast" (Salmon, 1989: 47). This explanation is intuitively unsatisfactory and fail to meet our expectations for what an explanation should be; nevertheless, it counts as adequate explanations under Hempel's D-N model of explanation.

One main, and controversial, features of Hempel's theory is the explanation/prediction symmetry, the so-called "symmetry thesis". According to Hempel-Oppenheim' article, there is, essentially, no difference between explanation and prediction. To predict something, we put together an argument and try to show that it is to be expected, though we don't know for sure yet whether it is going to happen. When we explain something, we know that it has happened already, and we show that it could have been predicted, using an argument containing a law. As Hempel and Oppenheim (1965 [1948]: 249) wrote: "Let us note here that the same formal analysis, including the four necessary conditions, applies to scientific prediction as well as to explanation. The difference between the two is of a pragmatic character." Let us analyze this thesis using the following example:

> (2) A falling barometer (together with the appropriate meteorological background knowledge or auxiliary assumptions) can reliably predict an approaching cold front. So, one may also be able to D-N explain the approach of the cold front by appealing to the barometer's drop. Nevertheless, we do not want to say that the barometric reading explains the storm, since both the drop in barometric reading and the occurrence of the storm are caused by atmospheric conditions in that region. When two different occurrences are effects of a common cause, we do not allow that either one of the effects explains the other. However, the explanation of the storm on the basis of the barometric reading fits the D-N model. So, we can **predict** the storm on the basis of barometric pressure, but we don't want to say that the storm is **explained** by the drop in barometric pressure. The moral of history is that many times we find two effects of a common cause that are correlated with one another. In such cases we do not explain one effect by means of the other.

Still in the counterexample of the asymmetry thesis, evolution enables us to provide well-justified and informative explanations, without predictions. Scriven (1959) that strongly attacked this thesis by citing evolutionary biology and asserting that it furnishes explanations (of what has evolved) but not predictions (of what will evolve), made this argument. As this was one of the first strong challenges to Hempel's account (Salmon, 1992), it will be important to clarify this criticism. Salmon (1989) criticized Scriven (1959) by considering evolutionary biology as a statistical theory. However, if we consider his exposition as the historical aspect of evolution, the opinions are sustained. The argument goes as follow. Evolutionary theory does not regard explanations as unsatisfactory because they do not enable the event in question to have been predicted (so being asymmetrical). Sriven then goes to criticize those who claim that Darwin didn't had the class that Newton had, because the principles of evolution are not in the form of universal laws and based predictions. Later he (1959: 478) is plain to show that knowledge obtained in evolution enables us to provide well-justified and informative explanations even without predictions: "… there will be cases where we can *explain* why certain animals and plants survived even when we could not have *predicted* that they would." Thus, explaining in evolutionary biology (as well as other in other areas) is to look for a cause.

> (3) John Jones (a male) has not become pregnant during the past year because he has faithfully consumed his wife's birth-control pills, and any male who regularly takes oral contraceptives will avoid becoming pregnant. Thus, this example fulfills the requirements for D-N explanation, but it manifestly fails to be a bona fide explanation.

The problem of relevance is illustrated by counterexample 3, however this example is more acute in the realm of statistical explanation than it is in connection with D-N explanation. So, in the next section we shall see what Hempel and Oppenheim had already noted, that not all explanations are of the Deductive-Nomological type. In 1965, Hempel published a comprehensive essay, "*Aspects of Scientific Explanation*" in which he offered a theory of statistical explanation encompassing two types: *deductive-statistical (D-S)* and *inductive-statistical (I-S)* model.

> (4) "If you reach for a cigarette and in doing so knock over an ink bottle which then spills onto the floor, you are in an excellent position to explain to your wife how that stain appeared on the carpet, that is, why the carpet is stained (if you cannot clean it off fast enough). You knocked the ink bottle over. This is the explanation of the state of affairs in question, and there is no nonsense about it being in doubt because you cannot quote the laws that are involved, Newton's and all the others; in fact, it appears one cannot here quote any unambiguous true general statements, such as would meet the requirements of the deductive model" (Scriven, 1962: 68). Thus, the conclusion from this statement is that it is possible to have perfectly good explanations without any laws. The covering law conception is not universally correct. This counterexample raises profound problems concerning the nature of causality (Salmon, 1992). Causality it will

be our main concern in the next topic. Before that, it is important to make clear what do we mean when the word “law” or “law of nature” is used.

One of the most vexing problems arising in this context is the characterization of law-sentences, i.e., the problem of distinguishing between lawful and accidental generalizations (Salmon, 1989). One of the main properties of a law is that it is not restricted in scope; it refer to objects anywhere in the universe at any time in its history—past, present, or future. Hempel and Oppenheim (1948[1965]) tried to give a formal definition of laws; however, they did not succeed in explaining the distinction between lawful and accidental generalizations (Salmon, 1989). Other author attempted to give others types of definitions: laws might be those generalizations that are used to make predictions, are invariable, function in explanations, and are integrated into the best systematization of the facts (Pfeifer, 2006). But, as Salmon (1989) argued, the problem of characterizing law-statements is one that has not gone away.

One of the main problems with the idea that there are natural laws is the argument provided by Weber (2005:6), who stated that laws “[C]ould be a relic from the theistic worldview that was popular during the formative years of modern science in the seventeenth century. In this worldview, God acted as a lawgiver in both the moral and natural realms. However, God has been banned from the explanations of natural science, and perhaps the concept of natural law should go with Him”. Finally, one major problem with the formulation made by Hempel and Oppenheim (1965 [1948]) is that their deductive logical structure of explanation captures effectively the Newtonian method of physical inquiry, the very method that has shaped the sciences in the modem era (Hon & Rakover, 2001), thereby bringing severe limitations in scope and applicability outside the physical science.

Before we proceed, I should remember the reader that, as argued before, the D-N model exposed by Hempel-Oppenheim (in contrast with the Inductive-Statistical model that was never mentioned by systematists) was developed in systematics mainly by Farris (1983) and Kluge (1999). Just as these four counter examples showed in combination, this approach does not work as a general model of scientific explanation at all. To make matters even worst, as systematics belong to historical sciences (more on this on chapter 10), this model performs even poorly. Within the fields of philosophy and logic, the Deductive-Nomological model fails when we include other elements of evolution, e.g., homoplasy as treated by cladists as mere error (more on this discussion on chapter 11).

4.4. Statistical Explanation

Carl Hempel's second thesis regarding *statistical explanation* is captured in the following statement made in his book (1965: 380): "By a *statistical explanation*, let us now understand any explanation that makes essential use of at least one law or theoretical principle of statistical form… there are two logically different types of statistical explanation. One of them amounts, basically, to the deductive subsumption of a narrower statistical uniformity under more comprehensive ones: I will call it *deductive-statistical explanation*. The other involves the subsumption, in a peculiar nondeductive sense, of a particular occurrence under statistical laws… it will be called *inductive-statistical explanation*." Thus, we shall see these models, alongside with Salmon *el al* (1971) model: Statistical-Revelance, which was intended to replace Hempel's models.

4.5. Deductive-statistical (D-S) explanation

The deductive-statistical (D-S) explanation, involves the deduction of "a narrower statistical uniformity" from a more general set of premises, at least one of which involves a more general statistical law. Since D-S explanation involves deduction of the explanandum from a law, it conforms to the same general pattern as the D-N explanation of regularities (Woodward, 2017). The statistical laws of empirical science and the universal laws are both general. Hence, Salmon (1984) suggested that D-S explanations is a subtype of D-N.

4.6. Inductive-statistical (I-S) model

In the case of I-S explanation, the *explanans* must include, essentially, at least one statistical law; as a result, it is impossible to deduce the *explanandum* statement from the *explanans*. Hempel therefore requires the I-S explanation to be an inductive argument that would render the *explanandum* predictable, not with deductive certainty but with high inductive probability, given the *explanans* (Salmon, 1989). Thus, an inductive-statistical (IS) model is an argument in which the conclusion is probable but not certain given the premises, and the premises are true and contain at least one statistical law of nature essentially. The idea of lawlike sentences thus has to be extended to account for statistical laws that have the conditional form $Prob(G/F) = r$, where r denotes the probability that an object of the set F is also a member of the set *G*. The set *F* is called the reference class of this statistical law (Weber *et al*, 2013). In its simplest form, an IS explanation is an argument with the following structure,

I-S P (G/F) = r
Fb
══════════[r]
Gb

The double line before the conclusion indicates that it is an inductive argument. The conclusion follows from the premises with high probability. In addition, “[r]” represents the degree of inductive support that is conferred upon the conclusion by the premises. This argument explains the fact that object b has property G by showing that this could be expected with probability r, given the fact that the statistical law L holds, and that b has property F. Another extra condition is what Hempel calls the *high probability requirement* (HPR). He requires that r is high without specifying exactly how high. For the sake of the argument and example, because, as Hempel (1965) argued, it seems impossible, without being arbitrary, to designate any particular number as the minimum value of the probability r permissible in an explanation, yest he assumed that r must always be higher than 0.5. Otherwise, we have an argument that makes us expect that the explanandum would not happen. In order to illustrate scheme I-S and the HPR, Weber *et. al.* (2013) constructed the following argument (this I-S explanation is set to the value of *r* at between 0.5 and 0.8):

L 81 % of the 12-18 year old inhabitants of Flanders has a smartphone
C Jan is between 12 and 18 years old and lives in Flanders
══════════[0,81] [makes practically certain]
E Jan has a smartphone

But how high is enough? How do we explain low probability events? Are they unexplainable? This perplexing question will be addressed by Salmon, and briefly discussed in the next section. One of the main difficulties with the (HPR) can be illustrated by a Mendelian genetic experiment on the color of pea blossoms made by Hempel (1965: 391-392). He showed to be highly probable that in a random populations of pea plants, each with its parent plants, represents a cross of a pure white-flowered and a pure red-flowered strain, approximately 75 per cent of the plants will have red flowers and the rest, white ones. Thus, these results can be explained by inductive-statistical model, because they are highly probable, and that was the case (we had 75 per cent of red flowers). Nevertheless, Salmon (1984: 86) stated that if we want to explain the white flowers, the answer is that "…there simply is no explanation; the event is inexplicable because it is improbable." Clearly, that is not the case, because we can explain equally well this event with high or low probability.

Hempel's main example of I-S explanation is the case of John Jones who recovered quickly from a streptococcus infection. When we ask why we are told that penicillin was administered, and that most (but not all) strep infections clear up quickly when treated with penicillin. This example is easily seen to fit the I-S schema set out above. As Hempel (1965: 381-382) writes: "But in contrast to the cases of deductive-nomological and deductive-statistical explanation, the *explanans* consisting of this statistical law together with the statement that the patient did receive penicillin obviously does not imply the *explanandum* statement, 'the patient' recovered', with deductive certainty, but only, as we might say, with high likelihood, or near-certainty." One persistent problem, is that it may be possible to formulate two inductively strong arguments with true premises that support contradictory conclusions.

As Salmon (1989) argued, an inductive argument, in contrast to deductive argument, strongly supports its conclusion may be transformed, by the addition of a new premise consistent with the original premises, into an argument that strongly undermines that conclusion. In this case, our available evidence provides us with a basis for two rival arguments, both of them inductively sound, whose "conclusions" contradict each other. This general problem with inductive inference motivated Rudolf Carnap (1962) to stipulate that correct measures of inductive support of a hypothesis can be made only in light of total evidence (his *Requirement of total evidence*). This is what Hempel (1966) referred to above as the *ambiguity of inductive reasoning*: inductively sound reasoning based on a consistent, and thus possibly true, set of "premises" may lead to contradictory "conclusions." This possibility is without parallel in deductive reasoning as the consequences deducible from any premises selected from a consistent set of sentences form again a consistent set. Hempel therefore proposed a modification to the model: the explanans must satisfy the *requirement of maximal specificity* (RMS). Namely, the *explanans* must include a law or theory based on all known relevant information available, in principle, prior to the *explanandum*-fact (Salmon, 1992). Back to the example of penicillin-resistant streptococcus, suppose, for instance, that the strain of streptococcus with which Jones is infected is known to be penicillin resistant. Putting in a formal scheme, the I-S explanation is as the following:

A patient with penicillin-resistant streptococcus who takes penicillin has a low probability of recovery.

Jones has penicillin-resistant streptococcus and takes penicillin (with high probability).

Jones does not recover.

Hence, we have two strong inductive arguments with compatible premises whose conclusions contradict one another. Finally, the general conditions of adequacy for scientific explanations set out in the first section of the Hempel-Oppenheim paper can be revised to encompass statistical explanation. Thus, we have four types of explanation (Salmon, 1992):

(1) Deductive-Nomological explanations of particular facts by universal laws.

(2) Deductive-Nomological explanations of general regularities by universal laws.

(3) Inductive-Statistical explanations of particular facts by statistical laws.

(4) Deductive-Statistical explanations of statistical regularities by statistical laws.

However, as we discussed, there is no need to distinguish type (2) from type (4). Explanations of general regularities by deduction from more general laws are the same in principle whether the laws involved are universal or statistical; we are thus left with two models, D-N and I-S. Finally, there seems to be general agreement that the ‘received view’ is not a viable model (Salmon, 1989).

4.7. The Statistical-Relevance Model of Explanation

In response to the I-S relevance problem found in Hempel’s requirement of maximal specificity, Salmon suggests, in a rather radical reconceptualization of the nature of explanation, that the factors cited in an explanation must stand in a relation of statistical relevance to the *explanandum*. So, consider now the following example elaborated by Salmon *et al* (1971). Suppose someone were to claim that large doses of vitamin C would produce rapid cures for the common cold. To ascertain the efficacy of vitamin C in producing rapid recovery from colds, we should note, it is not sufficient to establish that most people recover quickly; most colds disappear within a few days regardless of treatment. What is required is a double-blind controlled experiment in which the rate of quick recovery for those who take vitamin C is compared with the rate of quick recovery for those who receive only a placebo. If there is a significant difference in the probability of quick recovery for those who take vitamin C and for those who do not, we may conclude that vitamin C has some degree of causal efficacy in lessening the duration of colds. If, however, there is no difference between the two groups, then it would be a mistake to try to explain a person's quick recovery from a cold that result is attributed to treatment with vitamin C. This example shows that something must be done to exclude irrelevancies from scientific explanations. What is needed in addition is a requirement ensuring that *only* relevant information is included in D-N or I-S explanations. Thus, to say that a certain factor is *statistically relevant* to the occurrence of an event means, roughly, that *it makes a difference to the probability of that occurrence*—that is, the probability of the event is different in the presence of that factor than in its absence (Salmon, 1992).

Salmon (Salmon et al ., 1971; Salmon, 1984), developed the statistical relevance (SR) approach, that shows how such factors can be explanatory. In general, a factor C is statistically relevant to a factor B just in case $P(B/C) \neq P(B)$. The idea behind the SR model is that the presence of B is explained in a particular case by finding factors C that are positively relevant to B. The factors may be explanatory even if the probability of B given C is small. One important difference in relation to I-S is that according to the S-R model, no irrelevant factors should be included in an explanation. A problem with the S-R approach is that it admits explanatory factors that are correlated with the *explanandum* but that are not **causally** relevant. This problem can arise when the explanatory factor is correlated with the *explanandum* due to a common cause. Salmon (1984) himself ultimately became convinced that it was not possible to solve all of the problems associated with the S-R approach. Although the S-R pattern of scientific explanation provides some improvements over the I-S model, it suffers from a fundamental inadequacy: it focuses on statistical relevance rather than causal relevance (Salmon, 1992). In the earlier counterexample given, the correlation between vitamin C consumption and getting better from the cold; however, what we need is, in this case, a controlled experiment to find out whether taking massive doses of vitamin C is causally relevant to quick recovery from colds. Statistical relevance relation is evidence regarding the possible presence or absence of a causal relevance factor; **it is a causal relevance factor that has genuine explanatory import**. Before we enter this new topic discussing the various thesis about causality, it will be essential to expose other thesis about explanation (that do not appeal do causality or biology): the pragmatics of explanation (van Fraassen, 1980) and the Unification Account (Kitcher, 1989).

5. Other thesis about Scientific explanation

5.1. van Fraassen on Explanation and Pragmatics

There are some authors holding that there is no explanation without communication, and finding in the pragmatics of communication an account of many facets of explanatory practice. Among these philosophers is van Fraassen account of pragmatic explanation. According to Bas van Fraassen's book, *The Scientific Image* (1980), an explanation is simply an answer to a why-question; it is nothing other than descriptive information that, in a given context, answers a particular type of question. Whether a piece of information constitutes explanatory knowledge depends solely upon the context in which it is furnished. Thus, whatever distinction there is between descriptive and explanatory knowledge is entirely pragmatic (Salmon, 1989). While Hempel theorize about explanation as a relation between theory and empirical facts, van Fraassen comprehends it as a three-term relation, that is to say, a relation between theory, facts and **context**. Van Fraassen's thesis can be accommodated for various types of explanation (not just scientific explanation). Thus, an explanation is an answer to a why-question. Then: "… a theory of explanation must be a theory of why-questions." (Fraassen 1980: 134). Why-questions, for Van Frassen, are essentially contrastive. That is, they always, implicitly or explicitly, ask: Why Pk, rather than some set of alternatives X= ?

So, a why-question is conceived as a request for explanation expressed by an interrogation of the form "Why P ? " that emerges in a particular context, which depends on three factors: the topic P; the contrast class X = {P1, P2, …, P, …} and the relevance relation R. The contrast-class determines a set of alternatives to P. Let us see the following example made by Van Fraassen (1980: 127):

Why did Adam eat the apple?

This is the topic: a proposition expressing the fact whose explanation we are asking. But the same sentence can express different why-questions. This led us to more contextual factors. Thus, by the inflection or emphasis of the speaker, or by other contextual clues, we might find that any of three different questions is being expressed. It might mean,

Why did *Adam* eat the apple?

Here we have the issue of the contrast class, a set of propositions, including the topic, that determines the range of alternatives against which a why-question is asked. So, this contrast class = (Eve ate the apple, the serpent ate the apple, the goat ate the apple, etc.). At the same time, it might mean

Why did Adam *eat* the apple?

where the contrast class = (Adam ate the apple, Adam threw the apple away, Adam gave the apple back to Eve, Adam fed the apple to the goat, etc.). Also, it might mean

Why did Adam eat the *apple*?

where the contrast class = [Adam ate the apple, Adam ate the pear, Adam ate the pomegranate, etc.}. The context determines which is the appropriate contrast class.

Formally, a why-question Q is defined as follows: Q = <P, X, R>. Where Pk is the topic of the question, X = {Pi, P2, . . . , Pk, . . . } is the contrast class, and R is the relevance relation. The relevance relation R is the relation of cause to effect (Salmon, 1989). Thus Van Fraassen's thesis is that why-questions are why-interrogatives in their form, and in their way, are context-sensitive. Therefore, these questions express different why-questions in different contexts.

5.2. The Unification Account

For reasons of brevity, I will not describe Kitcher's (1989) technical apparatus in detail, but the basic idea of the unificationist account is that an explanation is a matter of providing a unified account of a range of different phenomena (Woodward, 2003). This view holds that scientific understanding increases as we decrease the number of independent assumptions that are required to explain what goes on in the world. The explanatory goal of this approach is the construction of a coherent world picture, and the fitting of particular facts within this framework. Explanations serve to organize and systematize our knowledge in the most efficient and coherent possible fashion. Understanding, in this view, involves having a world-picture and seeing how various aspects of the world and our experience of it fit into that picture (Salmon 1989). Thus, the theory that best unifies all the phenomena, then, might be said to yield the most for the fewest: the most derivable phenomena for the fewest number of basic principles. It is characteristic of the unificationist position to insist that only the absolutely most unifying theory has full explanatory power.

Theories that unify a range of different phenomena, previously dealt with by distinct theories, are in an obvious sense more general than these previous theories, and it is plausible that generality is at least sometimes an explanatory virtue. Whereas the unification approach is “top-down,” the causal/mechanical is “bottom-up." In Kitcher (1989: 430) words: “Top-down approaches will attempt to provide an account of what theoretical explanation is, use this as a basis for underwriting talk about ‘fundamental mechanisms’, and so proceed toward the identification of causes in particular cases. Bottom up approaches view us as having the ability to discern causal relations in specific episodes, and see theoretical explanation as stitching together results about the causation of individual states and events.” Essential for Kitcher’s (1989: 430) is the claim that “Science supplies us with explanations whose worth cannot be appreciated by considering them one-by-one but only by seeing how they form part of a systematic picture of the order of nature.” To achieving the following account: a successful explanation must belong to the so-called explanatory store E(K), where K is the set of statements endorsed by the scientific community, and E(K) is the maximally unifying systematization of K, that is, the set of derivations that employs fewer argument patterns than any other systematization of K. A generic form of the unification account, then, might require that an explanation of a phenomenon E do three things:

1. Present a theory T,

2. Present a sufficiently large and perhaps diverse set of phenomena P to which E belongs, and

3. Show that P can be derived in the right sort of way from T

Thus, Kitcher defines the degree of unification achieved by a derivation as a measure of how much smaller T is than P, where the size of these sets is deemed proportional to the number of independently acceptable lawlike sentences required to characterize the content of each.

Kitcher, following Hempel, regards that explanation must be structured in a deductive logic. Kitcher (1989: 448) calling himself a “*deductive chauvinist*” - that asserts that all explanation is deductive - and in part for this reason he endorses the view that “*in a certain sense*, all explanation is deductive” (1989: 448). However, contrary to Hempel, Kitcher considers that explanation is global, in other words, a deduction of why something was the case comes from some laws; so, in order to answer to the question why something happened, only arguments of the same form can be used to deduce many other deductive facts. To give a concrete instance of Kitcher’s idea, I shall describe the example that Khalifa (2013) used Thagard’s (2003: 244-255) schema:

“*External Pathway Explanation Schema:*

Explanation target:

Why does a **cell** become defective in a **function**?

Explanation pattern:

The **cell** is destructively affected by **external agents**, such as bacteria, viruses, or autoimmune cells.

These **external agents** operate by means of **pathways** that enable them to invade and disrupt the **cell**.

So, the **cell** becomes defective and cannot carry out its **function**.”

Thus, the boldfaced letters are variables that are filled in by different values. The unifying power of the schema is directly proportional to the variety of values that these variables can assume while still yielding correct instances of the explanation schema (Khalifa, 2013). Unificationist accounts have a number of attractive features. Plainly, there is some connection between explanation and unification, again on some understanding of that notion. In some areas of science (particularly physics) a drive toward unification is a very conspicuous goal of theory construction, and theories that are thought of as unifying what were previously seen as very disparate phenomena are seen as important explanatory achievements (Woodward, 2003).

5.3 Probabilistic Causality

By “Probabilistic Causation” we mean a group of theories that aim to characterize the relationship between cause and effect using the tools of probability theory. This is different from Hempel’s and Salmon’s approach, because they used probability to reach an explanatory answer, and herein, we are concerned to identify a cause - the probability of a cause. The central idea behind these theories is that a cause change the probabilities of their effects (Hitchcock, 2018). Even though Williamson (2009) argued that probabilistic theories are ultimately unsuccessful, we shall see some of these theories.

Most probabilistic theories of causality are motivated by the following central ideas: when A causes B the former raises or lowers the probability of the latter and this difference-making shows up in probabilistic dependencies between cause and effect (Williamson, 2009). Some authors maintained that probabilistic dependencies *characterize* the causal relation, i.e. provide necessary and sufficient conditions for causal connection, of the form: C causes E *if and only if* appropriate probabilistic dependencies obtain. For the example, the claim that prolonged exposure to formaldehyde causes nasal cancer does not imply that all or only those exposed to formaldehyde develop nasal cancer; instead, a cause need only raise the probability of its effect Hitchcock (2016).

Some of the theories that considered the above considerations was the one that require that causes raises the probability of their effects in all background conditions, as defended by Cartwright (1979) and Eells (1991); or whether causes must raise the probability of their effects in some background conditions and lower it in none, as proposed by Skyrms (1980). In recent years, some techniques have been developed for efficiently calculating probabilities from a Bayesian net[9] for constructing the match in the probability distribution of a dataset. Bayesian nets are often used to represent and reason with causal relationships. These approaches have proved very successful in artificial intelligence, and are now used in a wide variety of AI applications.

Causal models are mathematical models representing causal relationships within an individual system or population. They facilitate inferences about causal relationships from statistical data. The main and most discussed causal model is the causal Bayesian net. It uses causal diagrams, that represents simply dot-and-arrow pictures that summarize our existing scientific knowledge; to study a Bayesian network in which every arrow signifies a direct causal relation, or at least the possibility of one, in the direction of that arrow (Pearl & Mackenzie, 2018). A causal Bayes net uses a directed acyclic graph to represent causal relations among a set of variables, and pairs it with a probability distribution over the set of variables (Hitchcock, 2016). Thus, a causally interpreted Bayesian net is a net in which the arrows of the graph are interpreted as denoting direct causal relationships; this approach consists of a directed acyclic graph whose nodes are variables in the domain of interest, together with the probability distribution of each variable conditional on its parents in the graph (Williamson, 2009). The graph and the probabilities are tied together by a fundamental assumption known as the Markov condition: each variable is probabilistically independent of

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[9] "A Bayesian network is a representation of a joint probability distribution of a set of random variables with a possible mutual causal relationship... The main objective of the method is to model the posterior conditional probability distribution of outcome (often causal) variable(s) after observing new evidence" (Horny, 2014: 1).

its non-descendant conditional on its parents in the graph. Under a causal interpretation, the Causal Markov Condition says that each variable is probabilistically independent of its non-effects conditional on its direct causes.

5.4. Lewis' Counterfactuals account

David Lewis produced several different versions of a counterfactual theory of causation over the course of his career (Hitchcock, 2015), and for the sake of brevity, we will only discuss his first theory of causation (Lewis, 1973) and explanation (Lewis, 1986). First of all, we need to give a precise definition and clarification of what constitutes a counterfactual. Counterfactuals are subjunctive conditionals (as in "If Suzy had not kissed Billy, his cheeks would not have flushed"). They are used to talk about how things might have been, or how they must be. But what makes a statement about how things might have been, or about how things must be, true? The counterfactual theory rest on the notion of counterfactual dependence (Lewis, 1973). The simplest form of a counterfactual theory of causation is to say that, when we have two events C and E, "C causes E" is to be analyzed as "C and E occur, and if C had not occurred E would not have occurred" (Nolan, 2005). Accordinly to Lewis (1973: 8-9): "Counterfactuals are related to a kind of strict conditional based on comparative similarity of possible worlds. A counterfactual ϕ -> ψ is true at a world i if and only if ψ holds at certain ϕ -worlds; but certainly not all ϕ -worlds matter. ' If kangaroos had no tails, they would topple over' is true (or false, as the case may be) at our world, quite without regard to those possible worlds where kangaroos walk around on crutches, and stay upright that way. Those worlds are too far away from ours. What is meant by the counterfactual is that, things being pretty much as they are—the scarcity of crutches for kangaroos being pretty much as it actually is, the kangaroos' inability to use crutches being pretty much as it actually is, and so on—if kangaroos had no tails they would topple over."

The notion of possible worlds, thus, tells us that we should evaluate counterfactuals of this kind by deciding whether the possible world in which c and not-e, is closer to the actual world than the possible world in which *c* and *e* (Menzies, 2009). Lewis espouses a reality about possible worlds, according to which non-actual possible worlds are real concrete entities on a par with the actual world. Shortly, the central notion of a possible world for counterfactuals is a relation of comparative similarity between worlds; one world is said to be closer to actuality than another if the first resembles the actual world more than the second does (Menzies, 2009).

Lewis (1973: 84) defines possible words as: "… other than the one we happen to inhabit… I believe that things could have been different in countless ways … therefore [I] believe in the existence of entities that might be called 'ways things could have been'. I prefer to call them 'possible worlds'." So, a possible world, W1, is closer to the actual world than another possible world, W2, iff W1 resembles the actual world more closely than W2 does (so W1 is less of a departure from actuality than W2). Thus, Lewis defines a notion of causal dependence between events in the following way (Menzies, 2009):

Where *c* and *e* are two distinct possible events, *e* causally depends on *c* if and only if, if *c* were to occur *e* would occur; and if *c* were not to occur *e* would not occur.

If events *c* and *e* both occur, causal dependence of *e* on *c* is sufficient, but not necessary, for *c* to be a cause of *e*. Lewis defines causation as the ancestral or transitive closure of causal dependence between events that occur (Hitchcock, 2015).

To overcome this problem Lewis extends the causal dependence to a transitive relation by taking its ancestral. He defines a causal chain as a finite sequence of actual events c, d, e,… where d causally depends on c, e on d, and so on throughout the sequence. On Lewis's account (1973), one event causes another if they stand at either end of a chain of causal dependence (where that chain may have only one link). Causal dependence implies causation, but in principle there can also be causation without causal dependence. When B causally depends on A, and C causally depends on B, then A causes C even if C would have happened without A. (Nolan, 2005). Later, Lewis (1986) takes causal explanation of a singular event to consist in providing some information about its causal history. In most typical cases, it is hard to say of an effect e that its cause was the event c. Lots of things contribute to bringing about a certain effect. All these factors, Lewis says, comprise the causal history of the effect. This history is a huge causal net in which the effect is located. To explain why this event happened, we need to offer some information about this causal net. A full explanation consists in offering a whole causal net, but hardly ever this full explanation is possible, nor, Lewis thinks, is it necessary. Often, some chunk of the net will be enough to offer an adequate causal explanation of why a certain singular event took place.

6. Thesis of Causation and Explanation

6.1. The Causal-mechanical Theories

As a quick reminder, the statistical-relevance (S-R) model, elaborated in Salmon (1971), consists in explanatory scheme that consists not in an argument but in an assemblage of relevant considerations. On this model, instead of high probability, the amount of relevant information is what counts. However, Salmon (1984) argued that the S-R model could not long endure as an independent conception of scientific explanation, for it embodied only statistical correlations, without appeal to causal relations. Thus, in his new explanation model Salmon takes that scientific explanation "consists in exhibiting the phenomena-to-be-explained as occupying their places in the patterns and regularities which structure the world." In particular, causes explain their effects because a cause tells us why its effect happens. The explanatory strength of science comes from its insights into various causal processes. Information about such processes can be used to explain effects with reference to their causes. A scientific explanation is an objective account about causal connections between things (or events) in the real world. An explanation is both true and relevant if, and only if, it discloses the real causal structure behind the given phenomena. The most important proponent of this view is Wesley Salmon, who presented, as a first version, an elaborate theory of causal-mechanistic explanation in his *Scientific Explanation and the Causal Structure of the World*. According to Salmon, we need a causal theory of explanation because the "underlying causal mechanisms hold the key to our *understanding* of the world" (Salmon, 1984: 260).

Processes are fundamental to his thesis and have much greater temporal duration, in contrast to events that are relatively located in space and time, accordingly to Salmon. To illustrate the difference, Salmon considers the event of a sneeze and the process of a shadow of a moving cloud across the sky. A **process** is, then, capable of **transmitting a mark** if, once the mark is introduced at one spatiotemporal location, it will persist to other spatiotemporal locations even in the absence of any further interaction. Thus, causal process are those that are capable of transmitting information. In contrast, there are *pseudo-process* that are incapable of transmitting information. To distinguish between causal and pseudo processes, Salmon makes use of Reichenbach's 'mark criterion': a process is causal if it is capable of transmitting a local modification in structure (a 'mark') (Salmon, 1984: 147).

For a matter of exemplification, Salmon (1984) gave the following example: a good deal of attention has been given in the press to cases of leukemia in military personnel who witnessed an atomic bomb test (code name "Smoky") at close range in 1957. Statistical studies of the survivors of the bombings of Hiroshima and Nagasaki have established the fact that exposure to high levels of radiation, such as occur in an atomic blast, is statistically relevant to the occurrence of leukemia—indeed, that the probability of leukemia is closely correlated with the distance from the explosion. A clear pattern of statistical relevance relations is exhibited here. If somebody contracts leukemia, this fact may be explained by citing the fact that they were, say, 2 kilometers from the hypocenter at the time of the explosion. This relationship is further explained by the fact that individuals located at specific distances from atomic blasts of specified magnitude receive certain high doses of radiation. There is a **causal process** that connects the occurrence of the bomb blast with the physiological harm done to people at some distance from the explosion. High energy radiation, released in the nuclear reactions, traverses the space between the blast and the individual. Thus, at each end of the causal process, i.e., the transmission of radiation from the bomb to the person, there is a **causal interaction**. The radiation is emitted as a result of a nuclear interaction when the bomb explodes, and it is absorbed by cells in the body of the victim. Each of these interactions are causal. In undertaking a general characterization of causal explanation, we must begin by carefully distinguishing between causal processes and causal interactions. The transmission of light from one place to another, and the motion of a material particle, are obvious examples of causal processes. The collision of two billiard balls, and the emission or absorption of a photon, are standard examples of causal interactions. Interactions are the sorts of things we are inclined to identify as events. Salmon proposes to overcome traditional difficulties with determining the nature of the causal relation by treating causality as primarily a characteristic of continuous processes rather than as a relation between events. The theory involves two elements, **the production and the propagation of causal influence**.

The intersection that happens when two process intersect and undergo causally correlated modification is called by him as a causal interaction (Salmon, 1984: 171): “Causal processes are the means by which causal influence is *propagated*, and changes in processes are *produced* by causal interactions... The distinction between causal processes and pseudo-processes was formulated in terms of the criterion of mark transmission. A mark is a modification in a process, and if that modification persists, the mark is transmitted. Modifications in processes occur when they intersect with other processes; if the modifications persist beyond the point of intersection, then the intersection constitutes a causal interaction and the interaction has produced marks that are transmitted.”

Let us now give the formal formulations of these principles:

(1) The principle of mark transmission (MT) states (Salmon, 1984: 148):

"MT: Let P be a process that, in the absence of interactions with other processes would remain uniform with respect to a characteristic Q, which it would manifest consistently over an interval that includes both of the space-time points A and B (A * B). Then, a mark (consisting of a modification of Q into Q'), which has been introduced into process P by means of a single local interaction at a point A, is transmitted to point B if [and only if] P manifests the modification Q' at B and at all stages of the process between A and B without additional interactions."

Hence, for Salmon a causal process is one that can transmit a mark, and it is these spatiotemporally continuous processes that propagate causal influence. Second, there is the 'interactive fork,' where an intersection between two processes produces a modification in both (1984: 170) and an ensuing correlation between the two processes cannot be screened off by the common cause. Instead, the interaction is governed by conservation laws. Salmon calls this a causal interaction.

(2) The principle of causal interaction (CI) states (Salmon, 1984: 171):

"Let P1 and P2 be two processes that intersect with one another at the space-time point S, which belongs to the histories of both. Let Q a characteristic that process P1 would exhibit throughout an interval (which includes subintervals on both sides of S in the history of P1) if the intersection with P2 did not occur; let R be a characteristic that process P2 would exhibit throughout an interval (which includes sub- intervals on both sides of S in the history of P2) if the intersection with P1 did not occur. Then, the intersection of P1 and P2 at S constitutes a causal interaction if:"

(l) P1 exhibits the characteristic Q before S, but it exhibits a modified characteristic Q' throughout an interval immediately following S; and

(2) P2 exhibits the characteristic R before S, but it exhibits a modified characteristic R' throughout an interval immediately following S.

Enough from these formalities, I now shall describe other proprieties derived from his thesis. Salmon (1984: 142), borrowing an idea of Reichenbach's (1956), articulated a closely related idea in his principle of the **common cause** to accompany this theory of the propagation of causal influence (Salmon also analyses the production of causal processes). According to him, causal production can be explained in terms of causal forks, whose main role is the part they play in the production of order and structure of causal processes, and which are characterized by statistical forks. The principle of the common cause says that where we have two events, A and B, where (1) holds, and there is no direct causal connection between A and B, then we seek to explain this correlation by finding a third earlier event C such that (2) holds. Salmon (1984: 132) explain these approaches as follows:

> "Suppose we have events of two types A and B that happen in conjunction more often than they would if they were statistically independent of each other. For example, let A and B stand for color blindness in two brothers. There is a certain probability that a male, selected from the population at random, will have that affliction, but since it is often hereditary, occurrences in male siblings are not independent. The probability that both will have it is greater than the product of the two respective probabilities. In cases of such statistical dependencies, we invoke a common cause C that accounts for them; in this case it is a genetic factor carried by the mother. In order to satisfy the conditions for a conjunctive fork, events of the types A and B must occur independently in the absence of the common cause C - that is, for two unrelated males, the probability of both being color-blind is equal to the product of the two separate probabilities. Furthermore, the probabilities of A and B must each be increased above their overall values if C is present. Clearly the probability of color blindness is greater in sons of mothers carrying the genetic factor than it is among all male children regardless of the genetic makeup of their mothers."

For Salmon (1984) causal processes and interactions are not a statistical relation, but the conjunctive forks are. So, scientific explanation is a two-tiered structure, consisting of statistical relevance relations on one level and causal processes and interactions on the other. Finally, Salmon's thesis can be seen as three fundamental aspects of causality (Salmon, 1984: 179):

"1. *Causal processes* are the means by which structure and order are propagated or transmitted from one space-time region of the universe to other times and places;

2. *Causal interactions*, as explicated in terms of interactive forks, constitute the means by which modifications in structure (which are propagated by causal processes) are produced;

3. *Conjunctive common causes*-as characterized in terms of conjunctive forks- play a vital role in the production of structure and order. In the conjunctive fork, it will be recalled, two or more

processes, which are physically independent of one another and which do not interact directly with each other, arise out of some special set of background conditions. The fact that such special background conditions exist is the source of a correlation among the various effects that would be utterly improbable in the absence of the common causal back ground."

Using the mechanism that explains how neurons can conduct action potentials ("nerve impulses") along their axons (nerve fibers), Weber (2005: 21) gives a fine example of Salmon's thesis: "The mechanism of action-potential propagation provides such a causal structure: it states all the relevant causal relations that contribute to action potentials. These causal relations include, for example, the relations between the states of the various ion transporters and the concentrations of the different anions and cations on both sides of the membrane. Other sets of causal relations exist among different parts of the ion channel molecules, between the electric field component of the membrane potential and the voltage-gated channels, and so on. Once these causal relations are understood, the propagation of action potentials is explained."

In sum, Salmon's broad objective is to offer a theory that is consistent with the following assumptions (Dowe, 2000): (i) causality is an *objective* feature of the world; (ii) causality is a *contingent* feature of the world; (iii) should be (in principle) *time-independent* so that it is consistent with a causal theory of time; (iv) the theory should not violate Hume's strictures concerning 'hidden powers. However, Dowe (2000) encountered some very problematic counterexamples from Salmon's model, and I shall discuss it next.

6.1.1. Main objections to Salmon's model: one more case for counterexamples

As a basis for his discussion of this and other criticisms, Dowe (2000) formulates the key notions in Salmon's account:

I. A process is something that displays consistency of characteristics.

II. A causal process is a process that can transmit a mark.

III. A mark is transmitted over an interval when it appears at each spacetime point of that interval, in the absence of interactions.

IV. A mark is an alteration to a characteristic, introduced by a single local interaction.

V. An interaction is an intersection of two processes where both processes are marked and the mark in each process is transmitted beyond the locus of the intersection.

Accordingly, Dowe (2000) raises the possibility that the definitions of ‘mark’ and ‘interaction’ might be mutually dependent, rendering the account circular. The concept of a mark involves the concept of an interaction: a mark is a modification to a process introduced by a single interaction (IV). But the concept of an interaction involves the concept of a mark: an interaction is an intersection where both processes are marked (V). In short, the concepts of ‘mark’ and ‘interaction’ are mutually dependent, so that the account is circular. To mark a process is to interact causally with it so that a modification of its structure occurs. And to interact causally with the process is to modify its structure (i.e. to mark it) by means of a process, which is also marked (i.e. by means of a causal process). So, the definitions of causal interaction and of marking appears to be mutually dependent (Dowe, 2000).

Another line of criticism was brought up by Kitcher (1989). He presented the following example as criticism: “Suppose that a child traveling in the car puts an arm out the window and holds up a flag. The child’s action produces a modification in the shape of the shadow. The modification persists without any further interaction. Provided that the arm is not retracted, the shape of the shadow will continue to be different from what it would otherwise have been.” (Kitcher, 1989: 463). Kitcher saw three main problems with Salmon’s approach: (1) problems in distinguishing the genuine causal processes from other continuous spatio-temporal paths; (2) problems from the possibility of exploiting the inertia of some processes that can be fortuitously coordinated with pseudo processes to “mark” them; (3) Salmon’s conditions seem applicable only some cases (to ideal - elementary), so that it excludes many causal processes and it fails to exclude many pseudo processes. One problem with Kitcher’s analysis is that it relies on imaginary examples in relation to actual ones, and as argued by Hull (1989), the superiority of actual over imaginary examples in both science and philosophy of science is evident. Another argument raised by Hitchcok (1995) is the failure of Salmon to capture the relation of explanatory relevance. The argument is, roughly, that this theory does not give an adequate basis for determining which properties possessed by causal processes and interactions are pertinent to a given outcome and which are not. More on the consequences of these conclusion will be dealt in the chapter 7.

6.1.2. Correlation is not causation: Reichenbach's Common Cause Principle

We saw earlier that Salon relied heavily on the notion of the common cause to give basis for the explanatory approach. Roughly, this principle affirms that there is “no correlation without causation”. This is, in its most compact and general formulation, the essence of what has become Reichenbach 's Common Cause Principle. According to this classical tradition in philosophy of science, articulated especially by Reichenbach (1956) and by Salmon (1984), correlations are *always* resulting of causal relations. Thus, in the words of Reichenbach (1956: 157): “If an improbable coincidence has occurred, there must exist a common cause.” Later, he illustrates this principle using the following example (Reichenbach, 1956: 157): “Suppose both lamps in a room go out suddenly. We regard it as improbable that by chance both bulbs burned out at the same time, and look for a burned-out fuse or some other interruption of the common power supply. The improbable coincidence is thus explained as the product of a common cause. The common effect, the fact that the room becomes completely dark, cannot account for the coincidence.” The common cause hypothesis makes the correlation quite probable, whereas the separate cause explanation makes it almost miraculous (because it is very improbable). More explicitly, the Common Cause Principle says that every correlation is either due to a direct causal effect linking the correlated entities, or is brought about by a third factor, a so-called Reichenbachian common cause that stands in a well-defined probabilistic relation to the correlated events, that explains the correlation in the sense of entailing it. However, the Common Cause Principle does not rule out chance coincidences (the bulbs may burn out simultaneously); the existence of a common cause is not absolutely certain, but only probable. So, for Reinchenbach, common cause would it be a statistical problem.

After Sober (1988), the argument for the Principle of the Common Cause took the following form:

Given two correlated events E_1 and E_2, there is some prior event C which is a cause of E_1 and is also a cause of E_2, and which renders them conditionally probabilistically independent.

To say E_1 and E_2 become probabilistically independent to C means that C *screens off* E_1 from E_2. This can be explained using an example given by Salmon (1998): though the barometer drop indicates a storm and is statistically relevant to the occurrence of the storm, the barometer becomes statistically irrelevant to the occurrence of the storm, given the meteorological conditions that led to the storm and that are indicated by the barometer reading. There seems to be consensus among philosophers of science that the principle is not universally valid - the literature is full of counterexamples: correlations that are claimed to exist between causally unrelated events that do not admit common causes (Hofer-Szabó *et. al*., 2013). Others counterexamples come from correlations arising from conserved classical physical quantities such as momentum, by (Cartwright, 1988), and correlations predicted by quantum theory by Fraassen (1982). I will focus on the counterexample constructed by Sober (1987; 1988): the bread prices in Britain have been going up steadily over the last few centuries. The water levels in Venice have been going up steadily over the last few centuries. There is therefore a correlation between (simultaneous) bread prices in Britain and sea levels in Venice (Sober 1987). However, there is presumably no direct causation involved, nor a common cause. So, the correlation between Venetian sea levels and British bread prices as better explained by postulating separate causes. Furthermore, there is no general and *a priori* recipe for determining whether an observed correlation is of one sort or the other (Sober, 1988). The conclusion Sober (1987; 1988) reaches is that correlations do not always demands for explanation in terms of a common cause; he further suggests that the principle of the common cause is not an ultimate and irreducible component of our methodology. Arguing within a likelihood framework, Sober (1988) describes how the principle fades in respect to a phylogenetic inference. The principle shades some light about the dispute between phenetic measures and cladistic parsimony in the way that is quite devastating to Reichenbach's principle. If there are circumstances in which cladistics parsimony is to be used in preference to phenetic measures, then Reichenbach's principle is mistaken as a generality, because correlation at times will be the wrong basis on which to postulate common causes (between taxa). After all these criticism, Salmon’s model became to be regarded as problematic by various philosophers; even by Salmon himself (e.g., Salmon, 1998).

6.2. The Conserved Quantity Theory: counterexamples out, but explanation too!

Both Dowe (2000) and Kitcher (1989) have emphasized that one must invoke counterfactual notions not only in characterizing the concepts of causal processes and causal interaction but also in singling out the causal processes and causal interactions that are relevant to particular events. Hence, Salmon ended up changing his thesis - the major part of the motivation was an aversion to counterfactuals - as counterfactuals are notoriously context dependent. Thus, in more recent work, Salmon (1998) attempted to fashion a theory of causal explanation that completely avoids any appeal to counterfactuals. In this new theory which is influenced by the conserved process theory of causation of Dowe (2000), Salmon defined a causal process as a process that transmits a non-zero amount of a conserved quantity at each moment in its history. Conserved quantities are quantities so characterized in physics—linear momentum, angular momentum, charge, and so on. A causal interaction is an intersection of world lines associated with causal processes involving exchange of a conserved quantity (Dowe, 2000).

Dowe's theory makes use of the same general idea as Salmon's: causal processes are fundamental, and events are causally related if and only if they are connected by a series of causal processes whose intersections constitute causal interactions. However, Dowe (2000) sought to improve upon Salmon's theory by replacing the criterion of mark transmission by the requirement that causal processes possess a conserved quantity. The central idea is that it is the possession of a conserved quantity, rather than the ability to transmit a mark, that makes a process a causal process. Insofar as it links causation to quantities like energy and momentum, this account also bears some resemblance to the transference theory. Dowe (2000: 91) gives the following definition: "A conserved quantity is any quantity that is governed by a conservation law, and current scientific theory is our best guide as to what these are: quantities such as mass-energy, linear momentum, and charge." These conserved quantities are so characterized in physics: linear momentum, angular momentum, charge, and so on. Dowe's main objective is to distinguish causal from pseudo processes, and he does it by distinguishing objects that possess conserved quantities from those that don't.

The process theory of causality in terms of conserved quantities proposed by Dowe is based on the following definitions:

"Definition 1. A causal interaction is an intersection of world lines which involves exchange of a conserved quantity.

Definition 2. A causal process is a world line of an object which manifests a conserved quantity" (Dowe, 2000: 90).

Salmon endorsed Dowe's proposal and accepted a slightly modified version of it, according to which:

A process transmits a conserved quantity between A and B (A≠B) if and only if it possesses [a fixed amount of] *this quantity at A and at B and at every stage of the process between A and B without any interactions in the open interval (A,B) that involve an exchange of that particular conserved quantity*. (Salmon, 1997: 462)

Likewise, it is important that the conserved quantity be transmitted, and that a fixed quantity is transmitted in the absence of further interactions. Dowe emphasis the directionality built into transmissions, and attempts to rule out pseudo-process by identifying through time the object in question. Dowe (2000: 130) given the methodology of his theory of causality, to discern between truly causal explanations, by "…cause and effect are connected by a set of causal processes and interactions, where a causal process is the world line of an object that possesses a conserved quantity, and a causal interaction involves an exchange of a conserved quantity. If such quantities (energy, momentum, charge etc.) are the genuine properties, then the genuine positive events or facts involve the possession of those quantities." One important relation between both Dowe and Salmon is that, in their view, the Conserved Quantity theory is better than its predecessor because it manages to avoid any reference to counterfactuals. So far, so good. However, this theory has been put into scrutiny and exhibited some problems: (1) it rules out clear cases of causation, (2) that it lets in clear cases of non-causation (Schaffer, 2000) and it is an impractical theory (Woodward, 2003). I shall not give all the articulations and criticism of this theory, but it is very important to emphasize this is an unworkable theory; because it was strongly based on physicics, when it works, it only succeeds in some areas of the physical (or chemical) sciences. This is so because it fails to make it understandable how knowledge of causal relationships has any practical utility at all (Woodward, 2003). Now, I will show how another new model, the interventionist model by Woodward (2003), that is fully practictal to a working scientist (but for an experimental one and not a historical, see chapter 7), in a way that the Dowe's model could not.

6.3. The Interventionist Theory

In his highly influential book *Making Things Happen*, James Woodward (2003) - taking his ideas out of the social scientific and biomedical contexts - has put forward a manipulationist account of causal explanation. Although this not the only interventionist theory available, we will focus on James Woodward's interventionist theory of causation, because it is the most influential philosophical account of causation in an interventionist vein (Braillard & Malaterre, 2015). Briefly put, *c* causally explains *e* if *e* causally depends on *c*, where the notion of causal dependence is understood in terms of relevant (interventionist) counterfactual, i.e., counterfactuals that describe the outcomes of interventions. In other words, *c* causally explains *e* if, were *c* to be manipulated, *e* would change too. An intervention is a manipulation of the cause and it is assumed that the manipulation is, in principle, possible. As Woodward (2003: 10) argues: "The notion of information that is relevant to manipulation thus needs to be understood modally or counterfactually: the information that is relevant to causally explaining an outcome involves the identification of factors and relationships such that if (perhaps contrary to fact) manipulation of these factors were possible, this would be a way of manipulating or altering the phenomenon in question." Woodward model tell us that a relationship among some variables X and Y is causal if, were there an intervention that changed the value of X appropriately, the relationship between X and Y wouldn't change and the value of Y would change.

Let us consider an application of the interventionist theory of causation made by Reutlinger (2013). Suppose the causal claim that drinking coffee causes nervousness is true. Does this claim tells us more than the fact that drinking coffee is correlated with being nervous? Interventionists think this is, indeed, the case. Interventionists hold that drinking coffee causes nervousness iff, i.e., if and only if, there is a possible way to manipulate the coffee consumption (e.g. by serving only fruit juice in cafes) such that, as a result of this intervention, former coffee consumers would be less nervous. Let us describe, somewhat sketchily, the two key notions of intervention and invariance. A change of the value of X counts as an intervention I if it has the following characteristics:

a) the change of the value of X is entirely due to the intervention I;

b) the intervention changes the value of Y, if at all, only through changing the value of X.

The first characteristic makes sure that the change of X does not have causes other than the intervention I, while the second makes sure that the change of Y does not have causes other than the change of X (and its possible effects). These characteristics are meant to ensure that Y-changes are exclusively due to X-changes, which, in turn, are exclusively due to the intervention I. As Woodward stresses, there is a close link between intervention and manipulation. Yet, his account makes no special reference to human beings and their (manipulative) activities. In so far as a process has the right characteristics, it counts as an intervention.

The idea is that one ought to be able to associate with any successful explanation a hypothetical or counterfactual experiment that shows us that and how manipulation of the factors mentioned in the explanation would be a way of manipulating or altering the phenomenon explained, in other words, explanation in this model consists in answering a network of "what-if-things-had-been-different questions". One can identify conditions under which the *explanandum*-outcome would have been different, that is, information about changes that might be used to manipulate or control the outcome.

Thus, this model of causal explanation uses a counterfactual dependence between *explanans* and *explanandum* (provided the counterfactuals in question are understood appropriately) as the mode of retrieving information. Henceforth, we have the following conditional form: if there were an intervention such that the value of X was changed to some value x, then the value of Y would also change. In this sense, interventionist theories of causation are a special kind of counterfactual theory of causation (as Lewis' model explained above). Woodward links the notion of intervention with the notion of invariance. A certain relation (or a generalization) is invariant, Woodward (2000: 205) says, "if it would continue to hold—would remain stable or unchanged—as various other conditions change". What really matters for the characterization of invariance is that the generalization remains stable under a set of actual and counterfactual interventions. That would be Woodward way to avoid problems related to law statements, and he uses it as an auxiliary hypothesis that ought to remain the same thought the innervations. The main idea behind the interventionist account of causation is that causal relationships are revealed by the fact that when one intervenes on a given factor, while holding fixed other background conditions, one can observe what happens with the other element - learning the way that the variables chance its proprieties. Woodward's ideas capture the practice of experimental science, which is characterized by specific interventions, with replications, onto a framework that are placed in controlled experiments. Thus, for him (2003: 39): "[I]t is most perspicuous to think of causal relationships as relating variables or, to speak more precisely, as describing how changes in the value of one or more variables will change the value of other variables."

7. Conclusion on Scientific Explanation

7.1. Explanation and causality: Biology as a unique Science

After these brief expositions of these thesis, along with criticisms, what we need to do next is to draw some general conclusion to see if, regarding all these models, we can be able to pick up one and use in evolutionary biology, in particular, systematics. One general trend from our survey is the impression that the questions about explanation by philosophers of science has been given up to use biology as a model, but manly used physics (Braillard & Malaterre, 2015). For this reason, rethinking the relationships between the different models of biological explanation and of general scientific explanation is crucial. One point that should always be considered by biologists and philosophers as well is to recognize that many biological explanations are historical in nature. As philosophers and scientists now recognize, these explanations are obviously possible in the historical sciences; it takes the form of narrative explanations and although these are legitimate explanations, there are some problems with their evidential claims, as we are faced with the impossibility to have direct empirical access to these causal chains in some cases. Biology is also characterized by a lack of laws - same position supported by some philosophers (e.g., Beatty, 1995), despite the fact that others used a limited version (e.g., Brandon, 1996), that affirms that we have just contingent regularities in biology. Thus, explanation, mainly in the historical aspects of the evolution (like systematics) takes the form of a patchwork of different explanatory practices that are related to each other in complex ways that require clarification (Braillard & Malaterre, 2015). Before considering these issues, we should see what options we have for evolutionary biology, considering all those models of explanations exposed. In addition to the known problems in applying the nomological models of explanation (see section 4.3), biology by lacking natural laws was left outside the Deductive-Nomological thesis. Finally, I will show what virtues and problems each model presents, to finally argue for two promising models for Biology: the causal-mechanical of Salmon and the interventionist by Woodward.

(1) **van Fraassen on Explanation:** We will analyze the strongest objections posed by Philip Kitcher and Wesley Salmon (1987) against van Fraassen's account. The first is the one that do not impose enough constraints on the relevance relation R. Thus, the conditions that characterize why-questions and answers to why-questions must be supplemented by the further condition that R actually be a relevance relation; however, accepting this condition requires us to make a non-circular distinction between relevance relations and other relations and actually making this distinction amounts to facing very basic problems in the theory of explanation. Arguing for the failure of van Fraassen to address and solve matters of causality and laws, Salmon (1989: 146) concluded that: "[van Fraassen] has *not* succeeded in showing that all the traditional problems of explanation can be solved by appealing to pragmatics. In that sense he has not provided a pragmatic theory of explanation."

(2) **Probabilistic Causality:** As Williamson (2009) argued, the condition of Markov chain is oversimplistic: any probabilistic dependence can be fully accounted for by causal connections. As this particular physical interpretation of probability is adopted, under an actual frequency interpretation of probability, probabilistic dependencies may be entirely accidental, having no underlying explanation and in particular no causal explanation. Hence, causal relationships need not even be accompanied by probabilistic dependencies. Take the following example. When we read that smoking causes cancer, and it would not make sense to require that we clarify the claim by saying “smoking mechanistically causes cancer” or “smoking probabilistically causes cancer” since both mechanisms and probabilities are important evidence for this causal claim. This latter point is worth spelling out. If “smoking causes cancer” is to be understood in terms of a probabilistic relationship between smoking and cancer, then there is an epistemological problem: it is hard to explain why, given that there was excellent probabilistic evidence in favor of smoking being a cause of cancer, the causal claim was not generally accepted until a plausible physiological mechanism linking smoking and cancer was discovered. So, what we have here is that probabilistic claims are best viewed as factors worth pursuing in the direction of finding a cause, a mark, a mechanism, to be able to understand why ‘smoke causes cancer’. Hence, it is not the probabilities that tell us about the causal relationships but rather physical knowledge and physical mechanisms that link them (Williamson, 2009). One reason why mechanistic evidence is often required over and above evidence of probabilistic dependence is that causal claims need to be explanatory. Causal claims have two kinds of use: an inferential use, for making predictions, diagnoses, and strategic decisions, and an explanatory use, to give an account of why an effect occurred. Alternatively, in other words we need to make a clear distinction between two kinds of why-questions, namely, explanation-seeking why-questions and confirmation-seeking why- questions. Many years ago, Hempel (1965) made theses distinctions, that were further developed by Salmon (2001: 79), who argued that: “Explanation-seeking why-questions solicit answers to questions about why something occurred, or why something is the case. Confirmation-seeking why-questions solicit answers to questions about why we believe that something occurred or something is the case.” If Bayesian nets developed by Causal Markov Condition are correct, we need to conclude that Bayes’s theorem belongs to the theory of scientific **confirmation**, not

to the theory of scientific **explanation** (that is the same line of criticism given for abduction). Hence, in order to explain an event, one needs to invoke some kind of theoretical knowledge; physical connections among them and facts about the events and their linking mechanisms (Salmon 1998).

(3) **Lewis' Counterfactuals account:** For Lewis, Salmon (1989) raised two important shortcomings. First, the postulation of the existence of myriad possible worlds, distinct from our actual world, takes us deep into the superempirical. Second, evaluation of the similarity of possible worlds-which is essential to the analysis of counterfactuals-requires an appeal to laws, which is highly problematic as we have already seen. Hence, many philosophers of science have dismissed Lewis theory of causation and explanation that rely on counterfactuals as unclear or unscientific (Woodward, 2003). But, as a final note, his thesis was not very fruitful by itself, the thesis became the bases for the manipulationist account of explanation and causation. The manipulationist theory is a (species of a) counterfactual theory of explanation and causation, but differs in a number of ways from the counterfactual theories (Woodward, 2003); the asymmetry of overdetermination that, briefly, state that earlier events are massively overdetermined by later events, but not vice versa.

(4) **Unification account:** Two important classes of objections stand in the way of the unification approach to explanation by Woodward (2003). First his strategy of reconstruing purported nondeductive explanations as deductive is problematic. Second is the familiar question concerning the role of causation in explanation. Regarding the early problem, Kitcher fails to discard irrelevant information while providing an explanation. An explanation of an outcome must cite factors on which that outcome depends and possibly generalizations describing dependency relations in which the outcome figures (Woodward, 2003). These problems leads to the collapse of the: "…distinction between explaining why an outcome occurs and providing a reason for thinking that the outcome has occurred… premises that figure in a deductive argument that some outcome has occurred may fail to be part of an explanation of why that outcome has occurred and derivational structure does not automatically mirror explanatory or dependency relationships." (Woodward, 2001: 372). In relation to the role of causation, that it simply does not seem to be true that considerations of comparative unification always yield familiar judgments about causal asymmetries and causal irrelevancies; these seem to have (at least in part) an

independent source. Moreover, it casts doubt on Kitcher's contention that one can begin with the notion of explanatory unification, understood in a way that does not presuppose causal notions, and use it to derive the content of causal judgments (Woodward, 2003).

Before we proceed to scrutinize the models, one point must be clear: all of them may be said to fail for being internally inconsistent, and not by inappropriateness to biology. The following model developed by Salmon was already criticized; however, we shall see that if, even with critics, this thesis could survive, it could have heuristically value for evolutionary biology. Afterward, I will analyze the case of Woodward's model to see if it is relevant methodically in the two areas of biology: the experimental and historical (a detailed account of this differences is given on chapter 10 and table 1).

(5) **Causal Mechanical model**: Before we begin with our expositions, we need first, to remember that an appropriate model of scientific explanation should offer knowledge of the mechanisms of production and propagation of structure in the world. Thus, the knowledge of the mechanisms of production and propagation of structure in the world yields scientific understanding, and this is what we seek when giving an explanation-seeking why-questions. Essential to this (mechanical) view is the relation between the inference of causal events that are no longer available for our direct inspection. The "marks" that we can take as evidence of the distance past, even if they are partially destroyed (as in the case of paleontology), can still be used to postulate the adequate explanation-seeking why question of the determined event. Getting the fine grained (i.e., open the black box) details of the causal mechanisms that produced the fact to be explained is one of the main objectives of the thesis of Salmon. Later, we shall see that this property, is not found in the interventionist account; one the results of these facts, it will be argued, is that the model made by Salmon is, in potential at least, the model more appropriated (than the Woodward's, see next chapter) for the historical sciences, mainly whitin an evolutionary framework (including Phylogenetic Systematics).

(6) **The interventionist model**: This model is extremely adequate for experiments developed on population genetics that involves the production and experimental control of the environment. Ecology has also developed experimental technologies to understand some causal relation of taxa in its environment (Caponi, 2014) and this model of reasoning seems very adequate to study the causal complex relation

in ecological problems. It seems very straightforward the other experimental directed fields of biology, for example genetics: “New experimental and instrumental techniques have played such a decisive role in the development of molecular biology into an explanatory science precisely because such techniques make it possible to intervene in and manipulate biological systems and to observe the results in ways that were not previously possible” (Woodward, 2001: 9).” Otherwise to the historical sciences, that it is not capable of intervening or manipulating past causal events, is this successful framework maintained? In order to answer these questions, take the example of the extinction of (most) the dinosaurs. As the Avarez (see Cleland, 2002) hypothesis is accepted by scientists, a huge meteor caused their death. We know with high support the reasons for their death, but we couldn’t predict that this would happen, and we wouldn’t predict that this would be a condition for a radiative adaptation for mammals, that would lead to Hominidae and humans. Thus, we have achieved well founded causal explanation, “reconstructing past events”, while the prediction would be almost impossible. Woodward (2003) thinks it is possible to give a positive framework from this event. For that he used an approach called “what-if-things-had-been-different” questions (Woodward, 2003: 11): “[O]ne ought to be able to associate with any successful explanation a **hypothetical or counterfactual experiment** that shows us that and how manipulation of the factors mentioned in the explanation… would be a way of manipulating or altering the phenomenon explained. (my emphasis)”. Thus, for Woodward to construct a hypothetical experiment would be enough, heuristically useful, to think of causal and explanatory claims, even if actual manipulation is impossible. I argue here that this is not appropriate, because it conflates historical from experimental demands (see table 1); furthermore no explanatory depth is gained by exploring these hypothetical experiments that cannot be predict or manipulated. One of the main reasons this is what Gould (1989) called contingency: the minor changes in upstream conditions that have major downstream consequences, or the future is underdetermined by past, unpredictable events (in relation to the outcomes of evolutionary processes), that turns our ability to predict how Earth would look today if we could “replay the tape of life, very problematic at best” (Turner, 2015). In this context, an evolutionary explanation of past events is counterfactually dependent of the unpredictable outcomes of evolutionary processes, thus, this cast some serious doubts about how we could be able to causally explain historical unique events by Woodward thesis. Aligned with these discussions, Turner (2015: 79) argued that: “[I]t’s not entirely clear how to assess counterfactual claims about evolutionary history (e.g., ‘If this or that had been different in the past, humans would never have evolved.’)”. To sum up, while Woodward model is both philosophical and operational very strong and sound for experimental sciences, it is not so cogent in relation to historical sciences, mainly in the evolutionary process.

Finally, Salmon’s model could be the one used for evolutionary biology. It was argued that causal accounts of explanation have been offered as a solution to many of the problems traditionally encountered by nomological models (Salmon, 1984; 1998). It is clear that many explanations in biology do involve citing causes and some aspects of causal regularities (Braillard & Malaterre, 2015). One of the strengths of explaining a phenomenon in a mechanistic way involves decomposing a system at the origin of that phenomenon and its interacting parts, and giving a description of how the organization and activities of these parts are interconnect in order to propagate information to produce the phenomenon to be explained. So far, so good. But is it enough, for instance, to say that mammals are defined by possessing fur (their “mark” *sensu* Salmon)? Is this a process or an event? In a physical process, when we identify the process that can impose a mark, without further interventions, this mark will persist in from a posterior time; these processes are causal for the capacity to transmit marks (and information) as an indication of their causal nature. However, evolutionary biology has a strong explanatory force in their historical narratives that are not dealing with process, but with unique particular circumstances (Hull, 1992). Our history does not stop there: as argued by Ayala (2016) inanimate objects and processes are not directed toward specific ends and did not come into existence as a consequence of the purposes they serve, as in the case of the configurations of atomic molecules. However, features of organisms, like a bird’s wings, eyes, kidneys can be considered as having a purpose or goal: wings are for flying, eyes are for seeing and kidneys to regulate the composition of the blood. Thus, in all these examples it may be said that they are teleological because they have a design for a certain function, and can be identified as adaptations (more on this on chapters 8 and 9). Therefore, just a process and a mark is necessary, but it is also far from sufficient for evolutionary biology. Salmon’s model is heuristically weak because mainly (if not only) in biological sciences, particularly in its historical disciplines, like evolution, that teleological demands (and explanations) are legitime and necessary for evolutionary causal explanations. The transference of marks and information are simply not enough.

Another type of explanation that immediately comes to mind to a biologist is functional explanations, that were tradicionally dealt with in biology (see section 8.2). This is a central part of the explanation of organisms and its traits as it involves in their organization the concept of function. Traits are, then, explained by their function and this explanatory pattern is present in a multi-level (molecular to systemic). For achieving this explanation, it will be used **a derivation of an etiological theory of function**. This theory, the select effects theory, holds, roughly that a trait's function is whatever it was selected for, by natural selection or some comparable selection process, so being a teleological explanation. Even with some problems, Pigliucci & Kaplan (2006) argued that the etiological approach to functions (as the one developed by Garson) is the best one for understanding and interpreting the function of traits evolution in evolutionary biology. Garson (2019) in his so called 'generalized selected effects theory of function' tears down the widely held prejudice that natural selection, acting between organisms, is the only kind of selection process that matters for functions, a useful trait can, also, evolve by genetic drift or sexual selection, for instance. Therefore, when we speak of a well-confirmed functional explanation, we are given an evolutionary explanation for the existence of that same trait; why it evolved in that way? Because it was selected, from the ancestor to extant species, for that (history matters in this theory of function). This form of reasoning sheds some light on adaptation and related issues; this is so because, as it is now widely accepted, adaptation of a trait is maintained in the current population of individuals through the functions it acquired by historical association developed by natural selection - or by sexual selection (Pigliucci & Kaplan, 2006). In the following chapter, we will discuss some positive and constructive aspects of causally and explanation, because merely negative criticism is out of place. This makes room for the next section, i.e., 7.2, where we will introduce how teleological thinking is used in biology and argue for the close connection with functional analysis.

7.2. Causality and Explanation: What is left of it?

Causality, as originates in a category in daily life experiences, can lead laypeople to consider correlation as evidence of causation. However, as most elementary logic or statistics show us: Correlation is not causation. The rooster's crow is highly correlated with the sunrise, but it does not cause the sunrise. However, neither causation is (always) an explanation. The relation between both of these concepts are related, as argued, and we need to consider causation as the ontological counterpart to causal explanation (Faye, 2016). Only in this way that we can consider a causal explanation as expressing our understanding of a particular causal relationships in nature. As Hume (1748/1999) taught us, causes determine their effects; however, effects fail to determine their causes (this is the so needed asymmetry of explanation). And most importantly, he showed that there can be regularity without causation. Following this fact, we can say that neither pure logic nor epistemology alone can reveal causation, in other words, there is no universal way to get this kind of knowledge - this is what Russell (1913) argued on the "law of causality" being obsolete and misleading. Another characteristic is that all model of causation is physicalist in their argumentation, i.e., they all attribute some mind-independent empirical feature to causation - testable (in potential) evidential information - which a causal explanation has to grasp in order to have an explanation after all.

Explanation is an answer to a why question - as the framework of evolutionary biology (Dennett, 1995). Thus, discovering a cause can give us the explanatory information we need. The causal explanation is indubitably relevant to the explanation-seeking why-question (Salmon, 1998), as long as the cause is explanatory **relevant** for its effect since the effect would not have occurred unless the cause had occurred. Usually, we assume the complexity in the relation of thousands of causal relations that hold between our bodies and the objects in the world. Therefore, assuming these complexities, an idealized "complete" explanation (so that every relevant causal factor of an event is described), is clearly a dead end. Instead, all that we can do is to some pieces of the "complete" explanation that will be relevant to our hypothesis. Our context (van Fraassen, 1980) will be what will determine what and how much pieces of evidence we shall be given, in order for a satisfactory explanation. For instance, what kind and amount of evidence that an experimental science, like molecular biologist studying the transcripts of a particular gene; or that a historical science demands for giving a satisfactory explanation of the why a taxon radiated historically, as paleontologists hypothesize, would need? Thus here we have some plain examples for demands for plurality. Explanatory pluralism, i.e., the character of scientific explanation in which two explanations from different biological phenomena can be given (Brigandt, 2013), should be used to achieve an explanation by using different models within a discipline. Thus, as some of philosophers acknowledged - including Salmon - no single account captures all instances and aspects of scientific explanation. This is especially true in philosophy of biology, where different kinds of explanations are used in many disciplines across biology. Brigandt (2013) argues, for instance, that mathematical models and statistical explanations are very relevant as a heursitical tool in evolutionary biology and ecology; while causal-mechanistic explanations are used in experimental biology (e.g., physiology, developmental biology, and molecular biology). Therefore, we should not look for some single relation or model to discover what is involved in scientific explanation. Instead, we should realize that different model of scientific explanation is crucial to have a cognitively valid understanding. In this way, we can use some model to explain a simple phenomenon: mechanistic model of explanation, using the thesis of Salmon (for the paleontologist) or of Woodward (for the molecular biologist) together with some function explanation, so that we can, finally, have a more complete picture of an explanation of a pattern or phenomenon. And finally, as Lipton (2009: 29-30) resumed, we should pursuit well confirmed explanations because: “Better explanations explain more types of phenomena, explain them with greater precision, provide more information about underlying causal mechanisms, unify apparently disparate phenomena, or simplify our overall picture of the world.”

In the following chapters, I will develop a framework for explanation in systematics following the causal-explanatory role of functions that aims to give a causal explanation for the existence of traits (Garson, 2019). This analysis will try to provide a better understanding of the roles that a causal theory must present to present give a explanation in phygenetic systematics; in a way different from the general models of explanations that were criticized in earlier chapters.

8. Teleology: towards a new life in biology

8.1. Teleology and functional analysis: two sides of the same coin?

Our discourse and thought about the living world around us, about ourselves, our bodies, our activities, and about the things we make is run through with description and explanation in terms of goals, purposes and functions. We characterize things, such as organs and artefacts, and also social institutions, in terms of their essential functions and their efficacy in fulfilling them. We can explain morphology of an insect in terms of the purposes served by their form and features. We describe what it enables the animal to do, and how it affects the good of the animal or its offspring. For instance, the **function** of camouflage traits of many organisms is to conceal their presence, either from predators or from prey. These kinds of questions are called teleological explanations, and these kinds of answer to the question ‘Why?’ by reference to an end or purpose (*telos*).

To begin with, I will give a widely used example: what is the function of the heart? Usually we can find the following response: the heart beats in order for the blood go throughout the body via the circulatory system. However, this is for Maynard-Smith (1990: 66), the same as: “*'Those animals which, in the past, had hearts that were efficient pumps survived, because oxygen reached their tissues, whereas animals whose hearts were less efficient as pumps died. Since offspring resemble their parents, this resulted in the fact that present-day animals have hearts that are efficient pumps'. In other words, he is giving an evolutionary explanation for the heart beat, and not a physiological one*.” When we causally explain the function of the heart are we giving a teleological explanation? Before we can answer this question, we must explicate (*sensu* Carnap 1962) the term that we are trying to explain. In this way, we can define teleology as following (Cummins, 2002: 164): “*Teleology is the idea that some things can and should be explained by appeal to their purpose or goal or function… teleological explanation seeks to account for the existence or presence of a biological trait, or structure or behavior by appeal to its function*.” Therefore, biological functions can generate **genuine** teleological explanations, as they both they refer in talk of functions to the causal history of the traits that have the proper function (Neander, 1991).

Consider the following functional explanation provided by Stoddard *et. al.* (2017). The authors aim to propose an “adaptative explanation” for the size of the eggs (asymmetry and ellipticity) in various avian clades. They have found that these forms when correlated with biometric, life history, and environmental parameters, show that egg size is regulated and causally correlated by life history characteristics and spatial constraints in the nest. So, the form is functionally related to adaptations for flight (as a key driver). Stoddard *et. al.* (2017: 1253) further proposed that the “[G]eneral adaptations for strong flight select for a constrained, muscular, streamlined body plan in both males and females, giving rise in the latter, directly or indirectly, to asymmetric and/or elliptical eggs.” However, they made explicitly that the “[P]recise physiological mechanisms by which morphological adaptations for flight might affect egg shape are unknown.” So, it is plain to see that when they gave a functional explanation, the evolutionary (in this case adaptacionist) explanation was achieved as well. In this example, we can see that we are explaining a trait, the egg shape, by the ends, or function – in this case, selection for a strong flight – in this way, we are explaining something that is forward in time relative to the thing explained. This is exactly what a teleological explanation means in pursuit of an explanation. Thus, in biology, especially evolutionary biology, this kind of talk is commonplace and correct. In conclusion, the functional analysis is the **operational** way that we can study teleology scientifically - biological functions, thus, can generate genuine teleological explanations. It is obvious how teleology (with its forward-looking approach) is important for evolutionary biology; being one of the main reasons it distinguishes itself from the physical sciences (Ruse, 1989). As canonical example, the motion of the Earth around the Sun results from the laws of gravity, and this is the results of laws of nature; it does not exist to satisfy certain ends or goals. We can see that only teleological explanations, unlike nonteleological ones, make a distinctive talk of a means-to-an-end relationship in the explanation process, this characteristic being one of the main distinctive of biology as a natural science (Ayala, 2016).

The teleological language can be referred as a forward-looking discourse, and various biologists are troubled with this issue, so much, to the extent that they tried to add a "new language" - teleonomy (Mayr, 1974). Alongside with this, we have some two additional problems that notorious biologists (for instance, Simpson, Mayr and Ghiselin) saw in the use of teleology (Lennox, 1992): anthropomorphism (i.e., a planning agent external to the world reference to conscious - typically divine) and reference to a force immanent to the organisms (vital forces or "vitalism) beyond the reach of empirical investigation. However, as I already argued, teleology has shifted its meaning and focus from its pre-evolutionary form, and now it is in the position that it can be used and maintained without violating the principles of modern science. Furthermore, this shift is aligned with the three main bases of a successful modern biology as considered by Williams (1992): mechanism, natural selection, and historicity. Thus, mechanism states that every vital function is performed from systems that possess a causal net that can explained from physical and chemical studies (as opposed by vitalism); the other aspect is the assumption that the Darwinian process of natural selection accounts for all explanatory framework for the existence of adaptation in an organism (as opposed to rational plan or Larmarkins); and finally, that historicity - "[T]he properties of the organic world, from the total biota to minute parts of animals and plants, [that] are the results of unique historical contingencies…" (Williamns, 1992:6) is very relevant.

In the next section, I will briefly discuss the misunderstandings that both philosophers of science and biologists made that until today we can hear some prejudice against teleology, that are clearly misconceptions. After that, I will argue for the relation between function, adaptation and selection. Finally, I will discuss how functional analysis are being conducted in systematics and how we can reach an understanding in this way.

8.2. Teleology and Biology: a misguided beginning

I will begin this section with the following quote from Mayr (1992, p. 117): “Perhaps no other ideology has influenced biology more profoundly than teleological thinking.” Indeed, mainly more recently, this influence was mainly a negative one, being considered a great metaphysical reminiscent of a period before Darwin. For instance, Ghiselin (1994, p. 489) wrote that: “As a result of my work on Darwin I realized that teleological thinking was still exercising a pernicious influence…” Moreover, the same author goes further in his attack against teleology by bringing this discussion to the level of mytholog-ical, stating that (Ghiselin, 1994, p. 489): “The notion that Darwin somehow brought teleological thinking back into biology is a myth.” However, as it will be argued, this is far from reality. First, the “anthropomorphism” indicated earlier, is a chimera of Greek thoughts: the Platonic and the Aristotelian. The burden of the Platonic model is evident here, as, according to Lennox (1992), this thinking explicitly treats the natural world as the production of a divine figure, and the physical universe as the result of a rational agent. However, the mat-ters are very different when we consider the Aristotle’s approach to teleology. The reading of Lennox (1992) provided evidence that the Aristotelian thinking in teleology is very close the modern biological explanations, so, for Aristotle, scientific understanding is achieved when somebody can correctly answer the question “Why?”, and such answers involve the identification of its causes, because one knows that for one fact to be explained there may be a number of different answers, reflecting different causes. This can be exemplified by the following quote of Aristotle made by Short (2002, p. 326): ‘‘Except for the organism’s form ... none of the parts that contribute to the organism’s life would come to be or exist’’. Finally, Lennox (1992) concludes that for Aristotle the action of a rational agent is unnecessary, while this is not the case for Plato. Now we can see that this accusation was misguided as just a Platonic teleology recurs to a supernatural, or divine, interpretation, while Aristotle was free from this constrain, and actually, his thinking lead to a naturalistic approach without these drawbacks. Thus, his view in very approximate to the scientific teleology used today by biologist.

The Natural Theology is a form of the Platonic tradition of teleology (Lennox, 1992). Some well know authors, like William Paley or John Herschel, followed this idea and thinking after the Scientific Revolution and during the era of Enlightenment. This movement followed a widespread belief in the development of ever greater perfection in the world through the exercise of God's laws (Mayr, 1992). However, as it is widely recognized, the scientific endeavor broke with this tradition, and any theological thinking would be discarded a priori. The second accusation teleology received from biologists and philosophers of science is that it is principled in a vitalistic way. Before we discuss vitalism, we should define it properly: "[T]he vitalists position was that living organisms, unlike artifacts, are subject to the influence of vital force, which is independent of the body." (Morris et. al., 2000, p. 583). Thus, the vitalistic movement added to an unknown, and presumably un-knowable, factor, that usually (if not all of it) is untestable. Currently, from a biological and scientific point of view, vitalism became discredited and vanished from the discourse of biologists (Mayr 1982). Thus, rather than postulating a mysterious, unknowable vital force, there is a recognition that life is inside the realm of the chemico-physical laws (Mayr, 1982). As a final thought, we can make a new interpretation of Ghiselin's (1997, p. 294) criticism of teleology as being a "[V]ast burden of worthless metaphysical baggage." If instead, we eliminate the "burden of worthless metaphysical baggage" of anthropomorphism, theology, final causes and vitalism, then we can have a scientifically valid notion of teleology that can help biologists to understand and explain traits in organisms. One of these understandings is the case of adaptation; this is so because Darwin forged the notion of adaptation in terms of the ap-parent design of the organism as if for a common purpose (Gardner, 2009). Thus, the explanatory framework of Darwin is in relation to function as an explanation of adaptations. I intend to show how this vitalistic ideas made so much harm for the teleological notion in biology as accounted by philosophers of science (mainly the positivists). In a famous Manifesto (Neurath *et. al.*, 1929) made by the founding figures of the Vienna circle, biology was treated as a science with metaphysical problems. The authors identified this problem as the presence of vitalistic thinking, and reject it as a metaphysical thesis. This is so, because they insisted on the universal validity of the explanation model in physics, as this filed would be a mature science and an exemplary for all other sciences. As we argued, the problem with vitalism is undoubtedly true, and for a long time biology was regarded for most of these philosophers as an immature science (but I can cite other reason for this, for instance its inherently historical nature). Thus, as Salmon (1989) argued, one motivation for the investigations of the problem of teleological/functional explanation by Hempel and Nagel was in large part by the vitalistic doctrine in biology. Ernest Nagel, in his *The Structure of Science* (1961), made the most comprehensive investigation of teleological (functional) explanation in biology by a positivist. There, he argued that teleological explanations in biology could always be reformulated in non-teleological terms without loss of content. Therefore, he was struggling for excluding this term from sciences, even if the mode of analysis clearly are of a teleological form. Furthermore, Nagel (1961) alongside Hempel (1965) worked what they have called the **problem of functional equivalence** in biology, in terms of the Deductive-Nomological (DN) model of scientific explanation. Functional equivalence can be understood as distinct traits that have the same function. These problems were in the line that functional explanations that do not fit any of the logical patterns for scientific explanation, including those for inductive or statistical explanation, recognized by him - the received view (Salmon, 1989). This problem was exposed brilliantly by Salmon (1989: 30): “When we identify some item as fulfilling a function, we recognize that it is sufficient to produce some result in a certain situation. But usually we cannot claim that it is the only possible device that would fulfill that function. It is not necessary for the realization of the goal.” Thus, in biology, mainly evolutionary biology, we have numerous examples that fulfils this line of reasoning. As a straightforward example, take the adaptations of Arctic and Antarctic mammals and birds to the challenges of polar life. The animals can regulate their body temperature by growing a winter plumage (birds - except penguins) and coat of fur (mamals), or by relying on a layer of blubber to prevent heat (penguins). Each of these strategies have the function to protect from the cold, so they are functionally equivalent, and mainly, no law could follow it deductively.

Hempel (1965: 324) concluded his discussion of functional analysis in the following terms: “It remains true, therefore, even for a properly relativized version of functional analysis, that its explanatory force is rather limited; in particular, it does not provide an explanation of why a particular item *i* rather than some functional equivalent of it occurs in system *s*.” Thus, for Hempel, functional analysis cannot qualify as an admissible type of explanation, but at best, it has heuristic value. This is so because in functional explanation the *explanandum* is, given the conditions, **necessary** for the *explanans*, and his deductive nomological model, the *explanans* must be logically **sufficient** for the *explanandum* (DiFrisco, 2017). However, as showed, this mode of thought is in the wrong direction, because its failure in recognizing causal approach, stemming in part from certain famous counterexamples to Hempel’s Deductive-Nomological account of explanation. Functional explanations are, therefore, appropriate and necessary, as well as scientific, as Salmon (1982) argued, and any philosophical model of scientific explanation, which cannot accommodate functional analysis, is inadequate. Henceforth the functional analyses and teleology is considered a legitimate pursuit in philosophy and biology (for instance: Brandon, 1990; Ayala, 2016; Neander, 1991; Cummins, 2002; Ruse, 1989; Gardner, 2009; Garson, 2019).

8.3. Darwin, Teleology and Adaptation - a fruitful union

As shown, the teleological thinking was in a very bad shape in the early 19th century. The only two available options were: (1) a theological approach, as a supernatural explanation style, and the (2) vitalistic explanation, as an untestable metaphysical discipline. However, all of this has changed when Charles Darwin published his book, Origin of Species (1859), in it, he laid down the fundamentals of the evolutionary thought by natural selection, as being a goal-directed, teleological force. As one evidence of his teleological thinking, Lennox (2013: 136) cited a passage of Darwin that is clearly constructed in a teleological form. Darwin, as showed by Lennox (2013), is explicitly accounting for adaptations as a consequence of chance variation and natural selection. In that way, we can see the use of selection-based (teleological) explanation, that it is unlike any of the forms of teleolo-gy available to him at that time as discussed. Ayala gave a concise argumentation for this move:

> “Darwin accepted the facts of adaptation, and then provided a natural explanation for the facts. One of his greatest accomplish-ments was to bring the teleological aspects of nature into the realm of science. [He substituted a theological view by a scientific teleological one]. The teleology of nature could now be explained, at least in principle, as the result of natural laws manifested in natural processes, without recourse to an external Creator or to spiritual or nonmaterial forces. At that point biology came to maturity as a science” (Ayala, 2016: 121)

When Darwin re-invented teleology (Lennox, 1993), he opened a new road for the scientific problem related to functions in biology. Because Darwin considered an explanation of adaptation as the chief requirement of evolutionary theory (Gould, 2002), adaptation became a largely important matter from that day after (mainly for the architects of the Neo-Darwinian program). Before going any further, we need to answer what, precisely, is an adaptation? The term ‘adaptation’ derives from ad + aptus, that is, the process by which populations of organisms evolve in such a way as to become better suited to their environments as advantageous traits become predominant driven by natural selection; in other words, the study of adaptation aims to understand the fit between organismal form and function across the living world (Brandon, 1990). So, as Sterenly (1996) argues, the reasoning to detect an adaptation is the same of as functional reasoning.

The problem of adaptation is that: “[O]f transforming environ-mental (external) information into internal changes of form, physiology and behavior.” (Gould, 2002: 157). Thus, adaptation is for Darwin the primary subject for practical study of evolutionary mechanisms (Gould, 2002), as we can read from the following passage: “Over all these causes of Change I am convinced that the accumula-tive action of Selection, whether applied methodically and more quickly, or unconsciously and more slowly, but more efficiently, is by far the predominant Power." (Darwin, 1859: 43). Although natural selection was the most important evolutionary mechanism for Darwin (Gould, 2002), this was not the only process, as the following quote shows us: “[I] am convinced that Natural Selection has been the main but not exclusive means of modification.” (Darwin, 1859: 6)[10]. As Darwin wrote, we need to be aware that there are other processes that can generate diversity and modification, which are unrelated do natural selection . Closely related to this quote, I will show a widely famous case of methodological uniformity, that became known as the “adaptationist programme” by Gould & Lewontin (1979). In this paper, they argued that the only hypothesis being con-sidered by some authors in their studies of the evolution of traits is an adaptational one, by that, excluding any other hypothesis (e.g., developmental constraint). However, before exposing in details the points of this oft-cited and influential paper, I will show that, as argued by Dennett (1995), the paper of Gould & Lewontin is a “massively misread classic”. Many scientists thought of the paper written by Gould & Lewontin (1979) as a refutation of adaptationism; or even as a criticism of teleology. But this is clearly in error. For example, Heads (2009) and Gandcolas (2015) regarded the argumentation of Gould & Lewontin (1979) as a criticism of teleology; however, a close read can show us that it is not the case. Instead, if Heads (2009) and Gandcolas (2015) criticized the erratic notion of ‘preadaptation’, that would be correct. For instance, feathers can be ‘preadaptations’ for flight; however, this suggested terminology is very misleading as it treats evolution in a forward-looking process, anticipating the future needs of the organism (which is clearly a misguided approach and reasoning). This was the reason why Gould & Vrba (1982) proposed the concept of exaptation, briefly that characters that evolved for other usages (or for no function at all) and posteriorly merged with other charac-ters in order to reach their current function.

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[10] However, we should be very careful in stating this “pluralism”. Mayr (1983), in a response to Gould & Lewontin, said that nobody nowadays use the same “plurarism” as Darwin, because he accepted alternatives to natural selection, as the effects of use and disuse and the direct action of external conditions on organisms, that were com-pletely discarded as options by the architects of the modern synthesis.

9.1. The “hardened” Modern Synthesis: the centrality of adaptation

The Modern Synthesis of the 1930s and 1940s is a well know theoretical and epistemological union in evolutionary biology, being considered a canonical example of a paradigm shift - unification of research groups - in biology (Futuyma, 2005; Gould, 2002; Pigliucci & Müller, 2010). For the sake of brevity, I will simply provide the high-lights of these ideas (for a detailed historical analysis, see Mayr & Provine, 1980). The name of this movement is taken from Julian Huxley’s 1942 book, *Evolution: The modern synthesis*, which settled the conceptual structure underlying evolutionary biology and captured and synthesized all that was then known about evolutionary biology.

As Futuyma (2005, p. 14) synthetized, their program hold: “(a) that genetic variation in phenotypic characters arises by random mu-tation and recombination; (b) that changes in the proportions of alleles and genotypes within a population may result in replacement of genotypes over generations; (c) that such changes in the proportions of genotypes may occur either by random fluctuations (genetic drift) or by nonrandom, consistent differences among genotypes in survival or reproduction rates (natural selection); and (d) that due to different histories of genetic drift and natural selection, populations of a species may diverge and become reproductively isolated species.” Therefore, these are the principal claims of the evolutionary synthesis, and even though these principles have been extended, clarified, or modified since then, these are the foundations of modern evolutionary biology. But these extensions and modifications became so substantial that, recently, some authors set out a new evolutionary biology agenda, known as the *Extended Synthesis*. Their agenda accounts for particular fields of inquiry, such as Evo-Devo and phenotypic plasticity (West-Eberhard, 2003). This movement had their synthetic book as well, the Pigliucci & Muller’s (2010) *Evolution - the Extended Synthesis*. This program presents five main goals (Pigliucci, 2010): (1) emphasize the importance of the developmental biology; (2) to provide a ‘holistic’ view of species (as a criticism of molecular biology); (3) to incorporate and give more explanatory primacy of phenotypic plasticity, genetic accommodation, epigenetic inheritance as contributing factors to phenotypic diversity; (4) to include elements from computational biology and (5) to incorporate insights from evolvability, modularity and robustness. Thus, these elements must be added – while some other must be redefined, like (a) and (b) – from the old principles of the Modern Synthesis, as these are the results of the most recent research conducted in the various fields in biology.

Back to the consequences of the Modern Synthesis, Gould (2002) argued that the process of the “synthesizing” had two main phases: (1) integration (restriction) of Mendel and Darwin to a core discipline of population genetics, being the only model of hereditary and diver-sity that should explain all life forms on Earth (to the dismissal of other ideas as essentialism, inheritance of acquired characters, ortho-genetic trends, and saltationism (Mayr, 1982) and (2) the phase of "hardening", that reached to orthodoxy as they maintained the assumption that adaptation is an option to be ascertained to an a priori “assumption of near ubiquity”. Afterwards the adaptationist program was firmly established, and for some time we had the prevalence of the idea that the power of natural selection, as an optimizing agent, is executed through the conceptual breakdown of organisms into unitary characters, proposing an evolutionary explanation for each of them. This programme considers the constraints (allometry, pleiotropy, phenotypic plasticity) in the organism so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic traits (Gould & Lewontin, 1979), and other processes that could be considered, such as genetic drift, genetic constraints were considered as giving so low influence that they should be dropped from the discussion. To make one concrete example, consider the persistence of basic structural similarities across different taxa, as the neck skeletons of giraffe, man, and mouse. Even having very different ways of life, they all present seven cervical vertebrae (Williams, 1992). This striking persistence can be explained historically (descent from a common ancestor) not by natural selec-tion (that explains adaptation and diversity) but by this constraint. Thus, stabilizing selection should be called to make this explanation coherent (Sterenly & Griffths, 1999).

Arguing for the circularity in the adaptationist program, adaptive stories would be very easy to confirm, but very hard to falsify (Gould & Lewontin, 1979), and this is a hallmark of poor scientific hypotheses. The epistemological role is very plain: adaptationists regard the simple presence of a trait as a confirmation that it is an adaptation shaped by natural selection. The underappreciation of other factors as being relevant for the modifications on an organism was one of the results of the simplistic idea of selection acting more or less directly on genes (Pigliucci & Kaplan, 2000) - different genes for each aspect of the organism which can be separately molded by natural selection (one-gene one-trait approach) - was a serious issue at that time. In their same work, Gould & Lewontin (1979) described some “common styles of argument” by the adaptationists, that is, briefly: “[T]he failure of one adaptive explanation should always simply inspire a search for another of the same general form, rather than a consideration of alternatives to the proposition that each part is 'for' some specific purpose." (Gould & Lewontin 1979: 589). Therefore, after this work, which was considered as the "final proclamation of death" (Rose & Lauder, 1996) of the adaptationist programme, or orthodox Darwinism (Dennett, 1995), as known and endorsed by the architects of the Modern Synthesis, come to an end. Their criticism became known as the "just-so stories", as in the words of Gould: "[L]ewontin and I… would later call "just-so stories," or plausible claims without tested evidence, whereas other prominent trends couldn't even generate a plausible story in adaptationist terms at all." (Gould, 2002: 39). Thus, this would be an adaptationist scenario to "confirm" the proposed narrative of the adaptation of a particular trait. However, this way of thought some-times was so ample to include the origins of any kind of trait (Smith, 2016).

9.2. Nails in the coffin of adaptationism? The fall of naive adaptationism and the raise of the modern adaptationist program

For one side the "Panglossian Paradigm" was right in its criticism and forced the evolutionary biologists to be more cautioned by their evidence and their form of confirmation (he way it was conceived, it constituted a bona fide example of a confirmation bias). This moved the science of evolution and biology to a new level of coherency, because as any theory which intend to deliver a fully-fledged narrative history (teleological or adaptationist), must be consistent with the tenets of modern science. Therefore, if the hypotheses of adaptation are unfalsifiable and do not possess an (explicitly) criterion of accept-ability that is not circular, this approach is clearly not a very strong scientific endeavor. By incorporating those relevant data, it is possi-ble, then, to support or disconfirm a hypothesis of adaptation.

We should see the efforts made by Gould & Lewontin to ap-proximate one main branch of evolutionary research within a scientific rigor necessary for any serious field. Besides these epistemological issues, they introduced some ontological problems to be dealt with by those scientists - these being the existence of pleiotropy, epistasis and developmental constraints, which connect up the ex-pression of genetic variation among loci in nonlinear ways (Pigliucci & Kaplan, 2000). And finally, they gave some alternative hypotheses to be considered when discussing the explanation of a trait, like an explanation considering no adaptation and no selection or selection without adaptation. As Pigliucci and Kaplan (2000, p. 67) wrote it: "It is this synthesis of constraints (spandrelism) and selection (panglossianism) that is the key to a more sober and realistic understanding of phenotypic evolution." Afterwards, even committed adaptationists began to recognize these criticisms, as their discussion and claims of adaptation were much more cautioned (Amundson, 1996). Consequently, the problem that we are trying to explain, the apparent de-sign of organisms as a result of adaptation (Gardner, 2009), could be adequately answered.

So far, so good. However, one of the side effects of being one of the most influential and cited articles in evolutionary biology is that various authors have caricatured, misunderstood and even failed to appreciate their views properly. What happened next can be exempli-fied by the following quote by Rose and Lauder (1996, p. 2): “This paper [Gould & Lewontin, (1979)] had such a substantial impact on the fashions of evolutionary biology that the very term ‘adaptationism,’ and sometimes even ‘adaptation’ itself, became pejorative. To a significant extent, the term adaptation was banished from the lexicon of evolutionary biology, for fear of being associated with the dread adaptationism.”

It is plain to see that the criticism by Gould and Lewontin even though is correct, lead some authors to abandon the pursuit of adaptations. Accordingly, Dennett argues that some hypotheses of adap-tation were, indeed, handled by excess by some authors and deserves criticism, but we need caution because while:

> Adaptationist reasoning is not optional; it is the heart and soul of evolu-tionary biology. Although it may be supplemented, and its flaws repaired, to think of displacing it from central position in biology is to imagine not just the downfall of Darwinism but the collapse of modern bio-chemistry and all the life sciences and medicine. (Dennett, 1995: 238)

In the same view, Gans (1988) when arguing for the lack of rigor of some authors for giving adaptive explanations, raised the example of the putative explanations of why the “buffalo eat grass”; when the responses given are along the lines of because the "buffalo are adapted to eat grass" or "buffalo evolved to eat grass", we can see that no explanation at all was given - our “why-question” was not answered (to give an explanation in this case is to give an narrative explanation). The methodological error that the adaptationists make can be clearly pointed by the following quote made by Mayr (1983) when he asks: "What is the function of a given structure or organ?” in this way, he already assumes adaptation; we just have to do discovery it. However, when we ask, “Does this trait have a function?” there is no assumption, a priori, that the trait is an adaptation (Llody, 2015). Thus, we should start our determination of the evolution of any trait by asking whether it is causally related to a certain function, only afterwards we can give any proposition of its adaptiveness.

In the next twenty years since the fall of the naïve adaptationism, we had what by Rose and Lauder (1996) called "Post-Spandrel Adap-tationism" or "The New Adaptationism" in which they set the new agenda for adaptations, selection and historicity (narrative explanations). This movement became also known as the "Adaptive-historical thinking" by Griffiths (1996), because he identified, along-side Rose and Lauder (1996), a historical turn, with its new tools and stronger methodologies, that were incorporated in the studies of adaptation. Within this scenario, Rose and Lauder (1996) showed the new assumptions that must be considered for future analysis that evolutionary biologists must pursuit in order to study selection and adaptation: (1) the use of phylogenies in the comparative method, that provided the critical evaluation and questions about the nature of homology, and looks rigorously at morphological data of all sorts (it is able to give a reliable hypotheses if the determinate trait is an evolu-tionary novelty - apomorphy - or if it is a homoplasy (e.g., convergency)); (2) the use of population biology through the development of methodologies based on quantitative genetics theory that involves selective manipulation that can replicate extant differences among populations; and (3) the rigor of functional morphology and biomechanics (as disciplines whose goal is the analysis of biological design and teleology). Thus, by correcting some methodological mistakes ("just-so stories" and the adaptationist programme), and introducing new coherent ones (The New Adaptationism), adaptational studies got a breath of fresh air, and can, finally, present unbiased and well-confirmed hypothesis. The inherent difficulty to propose a strongly supported hypothesis of adaptation will never be gone, however; as these are historical hypotheses that can be very hard to grasp because its evidence, the morphology and the environment of the organism, can change so much as a result of the passage of time, that the hypothesis can be undetermined in some cases. Even with these difficulties, the pursuit for adaptation is a very legitime one and is the core of the evolutionary biology, and the fact that evolutionary processes are not easily testable, should not be an epistemological excuse to give up to research it altogether (no one ever said science was easy). Using these criteria as weapons, scientists can formulate scientifi-cally testable and non-speculative argumentation in favour of adapta-tion, and as the next section aims to demonstrate, can make the teleological thinking legitime.

The cladistics revolution in the 1960's and 70's were a major step forward for studies of adaptation. Later, function analysis and adaptation were discussed in phylogenetics (Cracraft, 1981; Coddington, 1988; 1994; Lauder, 1981; 1990; Larson & Losos, 1996; Baum & Larson, 1991; Grandcolas, 2015). And, very importantly, all of these authors stressed out the widespread idea that natural selection is the **only** satisfactory explanation of adaptation (including the complex ones), even if constrain is available, and some features of organisms are not adaptations. Finally, the importance of Phylogenetics can be seen in the argumentation of Caponi (2012), which affirmed that an evolutionary explanation is an explanation of character states. Thus, Caponi (2012) continues, the explanation of apomorphies can be the forces of natural selection, sexual selection or genetic drift; while plesiomorphies have resulted from common descended or constriction[11].

A point of clarification is needed before proceeding. Before I introduce the issues regarding the uses of function explanation in systematics and its relations to teleology, it is very important to make a taxonomy of classes of inquiry derived from these three approaches stressed out by Rose & Lauder (1996). For instance the phylogeny is related to macroevolutionary studies, hence keep some epistemological and ontological peculiarities that pertain to the **historical sciences**; while the population biology, a field with microevolutionary implications, presents other methodological issues that are the broad area of the **experimental sciences**.

10. History and evolution

10.1. Evolutionary Biology as a borderland between Historical (macroevolutionary) and Experimental (microevolutionary) Sciences

I will introduce this theme by making a brief analysis for what are the kind of evidence that we can use for using inferences and confirming hypotheses and by critically evaluating the differences that are supposedly attributed to microevolution and macroevolution.

10.2. History Matters: A plea for Historical Sciences

Evidence, broadly defined as any kind of observation, observational report, experiential input, empirical information, or datum (Psillos 2007), supports or tells in favor of a given theory (or hypothesis), or as it is commonplace in the scientific discourse, it confirms that

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[11] As the concepts of apomorphy and plesiomorphy are relatives to a clade and its position in the history of taxa ("position in a tree"), we can say that the same character state can be regarded as originally derived from natural selection and, later, becomes maintained by common descent. Thus, these concepts are reciprocally (causal) related and do not exclude each other.

theory. On the other hand, evidence that tells against a theory disconfirms it. Thus, evidence is what makes one's hypothesis to be correct (or at least more probable), and gives one a reason for believing it (Achinstein 1978). One of the most famous methodologies to infer the evidential support of a hypothesis is the hypothetico-deductive model (H-D), that is plainly: to form a hypothesis on the basis of the available evidence (along with any auxiliary hypotheses) and if empirical predictions, that are deduced from that hypothesis, turn out to be successful, it is confirmed. However, the modern roots of the H-D method are, actually, closer to those of the falsificationist methodology; then the H-D method is viewed as hypotheses that had undergo severe tests, and if the predicted facts fail to obtain, we reject the hypothesis as falsified (Popper 1934/1959). However, sometimes scientists, in the face of a particular evidence, are unable to decide conclusively which theory to believe in relation to a rival one, so that the theory is considered to be underdetermined by the evidence (Stanford, 2017). Therefore, we can see the questions relating to evidence are far from trivial. One issue that is equal to these discussions is in relation to the evidence that are used for scientists. The physical and biological sciences are all empirical. This means that their assertions must ultimately face the test of observation by the evidence, but adding to the problems already showed, we could add the problem of the different types of evidence that are used in science. One of these differences are related to the Experimental and Historical Sciences (Cleland 2002, 2011; Currie 2016; Forber & Griffiths 2011; Gould 1989; Hull 1992; Jeffares 2008; Mayr 1982; Tucker 2009; Turner 2007). Gould (1989) was one of the main exponents of the pragmatical nature of these differences, thus, he makes a “plea for the high status of natural history”, but laments the fact that people so often associate the experimental method with the scientific method, and downgrades the epistemological aspects of the historical sciences. Sadly, Gould’s views were virtually ignored by biologists and philosophers. The things changed, mainly, when the work of Cleland (2002) became well known. She argued that historical scientists, in contrast to experimental ones, exhibits a distinctive arrangement of evidential reasoning (Cleland 2011, p. 554): “(i) the proliferation of multiple competing hypotheses to explain a puzzling body of traces encountered in fieldwork, and (ii) a search for a ‘smoking gun’ to discriminate among them”. Pivotal to Cleland’s analysis in the notion of a “smoking gun” that in her words (Cleland 2002, p. 481): “[I]s a trace(s) that unambiguously discriminates one hypothesis from among a set of currently available hypotheses as providing “the best explanation” of the traces thus far observed.” This is in relation to the total evidence available in a certain time for the evaluation of rival hypotheses. This is so because these historical hypotheses are very sensitive to the problem underdetermination of theories by the evidence. As historical evidences (e.g., fossils) decay through time, and may even disappear, it is needed, sometimes, only a small amount of them to arrive at a sufficiently accurate explain (reconstruct) what happened; this is what Cleland named as the "asymmetry of overdetermination". As a matter of clarification, and following Cleland (2002) and other authors, the next table (table 1) will concisely point to the main differences between the Experimental and Historical Sciences.

Many experimental scientists, however, relying in the Popperian H-D model argued for their apparent superiority to the historical science (Cleland 2001, 2002, 2009). Although presenting an intuitive appeal, the falsificationist (and the confirmational) scheme of the H-D model presents some straightforward problems that, for more than 60 years, was discussed by philosophers that considers it logically flawed (e.g., Putnam 1974; Salmon 1967; Stamos 1996; Sankey 2008; Sober 2000; for an earlier criticism of Popper's philosophy see Neurath 1935), historically inaccurate (e.g., Kuhn 1970; Laudan 1977), and imprecise to the practices of historical, as well as the experimental, scientists (e.g., Cleland 2002, 2011; see Stamos 2007 for a discussion in biology). To scrutinize and discuss in detail all the problems with this approach is beyond the objectives of this essay, thus I shall limit myself to point out that the H-D model cannot be used to support the claim that historical research is inferior to the experimental (Cleland 2001; 2002; 2009) and that the evaluation of historical hypotheses by the means of falsificationism version of the H-D model is flawed (Cleland 2002; Hull 1992; Tucker 2009; Turner 2007). Finally, following the complexity and holistic nature of science, there are some fields of science that include both sciences, as it is the case of evolutionary biology (Pigliucci 2013) that will pertain my discussion herein.

Thereby, Hull (1974) made a distinction between the evolutionary process and the phylogeny, in this way, distinguished the statistical (ahistorical) part from the non-statistical (historical). As a general and brief characterization, the process of evolution can be regarded as the field of the microevolution (more on this later), using disciplines as the genetics of population, and studies on the changing in frequency in the alleles in relation to natural selection and genetic drift. For instance, using a maximum-likelihood parameter to estimate the mitochondrial DNA in relation to the protein-coding genes, Paland and Lynch (2006) were able to support the hypothesis that sexual reproduction may accelerate the rate of adaptation that inhibit the accumulation of mildly deleterious mutations in populations. Those types of evidence are herein considered to belong to an experimental science. In relation to the "description of phylogeny" (Hull 1974), we can give the example of the historical narratives and the characters in a phylogenetic study. A straightforward example is the phylogenetic tree showing a hypothesis of the genealogical relationships among taxa base on evolutionary unique traits. Since the history of taxa, and homologues, with its evolutionary history in the Earth is unique, no standard statistical analysis is required. Thus, clearly within the scope of historical science. In order to scrutinize the differences between the historical and experimental differences in evolutionary biology, I will discuss two well know subjects in the area: the dichotomy of Microevolution and Macroevolution and study of adaptation as a matter of population biology and as a phylogenetic problem.

A matter of epistemology: the case of Microevolution Vs Macroevolution

Cleland's framework is particularly helpful for an evaluation of the epistemic status of an old and persistent dichotomy: macroevolution Vs microevolution; more precisely, whether macroevolution involves special higher-level mechanisms in relation to microevolution (or the evaluation that macroevolutionary processes is irreducible, and cannot be reduced to microevolution). As a matter of clarification, we should give two canonical examples that are usually attributed to either process: the famous case study of peppered-colored and black-colored moths in industrial England, that is attributed to microevolution and the so-called "Cambrian explosion", a rapid diversification of animals in the Cambrian (530 million years ago) that give rise to a multitude of new species that probably arose as a result of punctuated equilibrium (Erwin, 2009) and is thought to be due to macroevolution. Usually, the discussion is always directed to the issue if macroevolution ontologically depends on microevolution (Grantham 2007, Erwin 2009, Dietrich 2009). Those authors that advocate in favor of this distinction favor two lines of evidence that macroevolution differs ontologically from microevolution: the argument of a emergent nature of species-level fitness and the phenomena of the mass extinction as a representation of a quantitatively and a qualitatively different phenomenon (Grantham 2007; Erwin 2009). However, clearly, these are not ontological questions. Emergent traits and extinctions occurred in the long past, and are occurring now and very probably will continue in the future. The real problem here is how do we obtain this data and confirms that our hypotheses is a matter of emergency or extinction. In other words, the issue here is an epistemological one.

To make a concrete example, let us examine articles about extinctions. Extinction and its consequences to what has been called "sixth mass extinction" (Ceballos et al. 2015) are underway. They based their analysis on exceptionally high rates of modern extinction by

Table 1. Overview and comparison of the methodological and evidential differences between Experimental and Historical Sciences (Jeffares, 2008; Cleland, 2002; Tucker, 2009; Forber & Griffith, 2011).

	Experimental Sciences	Historical Sciences
Epistemic goal	To understand the repeatable regularities in the world (focus on a single, complex hypothesis; control for extraneous factors)	To understand spatially and temporally restrict events (to bring out a coherent and testable causal nexus)
Ontological possibilities (the problem of access of information)	Direct test of observation (able to interfere and repeat observations)	Indirect test of observations (uses "traces from the past")
Criterion of acceptability	Confirmed predictions (underdetermination of experimental results by test conditions; aims to dismiss false positives and negatives).	Coherent causal relations (common historical cause; use of consilience of multiple independent lines of evidence)
Quality of evidence	Evidence remains intact (can be accessed again)	Historical processes degrade and destroy a great deal of information about the past (e.g., fossilization and extinction)
Methodological emphasis	Laws and regularities; frequent use of statistical tests (stochastic approach)	Particulars, many times presents the structure of a historical narrative (complex and unique entities); rare use of statistical tests ('determinist' approach)

directly considering the data given by the International Union of Conservation of Nature (IUCN); thus, they recorded that 338 vertebrate extinctions have been documented since 1500. This survey in a good example of the characteristic of experimental sciences. But this confirmation can be obtained from the historical sciences as well, by using pieces of evidence that an event of extinction occurred using indirect inferences from the fossils and characters from Earth biota. As an example, take the Permo-Triassic extinction; a mass extinction at ~252 million years ago, that represents the most catastrophic loss of biodiversity in geological history

(Clarkson et al. 2015). The direct cause of this mass extinction is due to a diverse range of mechanisms, including widespread water column anoxia, euxinia, global warming and ocean acidification (Clarkson et al. 2015). Hence constituting a consilience of different hypotheses (Laudan, 1971), that collectively, supported the hypotheses that the ocean was acidified (as a cause of the extinction). The causal nexus was them constructed as a confirmed test evidence, namely, that if the acidification were true we will need confirm the existence of the following evidence : a pyrite-rich lithofacies in Permo-Triassic boundary sediments as evidence for anoxia; the decline of carbons isotopes as collapse of primary productivity (mass extinctions); increase in the calcium concentration of seawater, as a evidence of ocean acidification; concentration of a photosynthetic pigment produced by green sulfur bacteria as evidence of anoxia and euxinia (mass death of these organisms because green sulfur bacteria require sunlight and hydrogen sulfide to conduct photosynthesis, and this was very low around the time of the main extinction) (Payne & Clapham (2012). In sum, we can obtain the same degree of confirmation of extinction of life on Earth both from early times or today, the lie on the different form of inferences (e.g., one is directly observably while the other is indirect).

10.3. A breath of fresh air - the modern relations between function and systematics

The comparative method of biology brought up homology studies - that is regarded as the hierarchical basis of comparative biology (Hall, 1994) - to a new standard. As argued by Larson & Losos (1996), a principal answer and resolution of the old problem of delimiting arbitrary characters that are, without further analysis, considered as homology and unique to explain it origins, are the principles of phylogenetic analysis. This is so because study of homology (with the congruence of characters) addresses this criticism by providing objective criteria for identifying homologies - and homoplasies, including parallelism and convergence - as nonarbitrary components of organismal phenotype. Another principle that phylogenetic systematics can be important is in relation to the context in which a hypothetical character is simply a structural consequence of organismal architecture, development, and allometry (Gould & Lewontin, 1979); that is the old problem of the independence of characters. Even though Larson & Losos (1996) wrote that phylogenetic trees enable one to examine the historical associations of characters to identify cases of evolutionary nonindependence. Instead, we can regard it as an indirect evidence that dependence of characters was the case. Take the following example, if we have a high number of synapomorphies that confirms a certain clade, and we have suspicions that they are dependent, because they are related to constrains or design (as a matter of form-function), we should have a hypothesis of dependence higher than of independence. As is the case with most scientific problems, this initial procedure represents only a first orientation. In possession of this evidence we should conduct a new research for this case, in other words, to show compelling evidence that they are truly dependent (e.g., developmentally or genetically independent). It is very important to note that if we do not have a phylogenetic tree, we should not be even aware of these, probably, dependence characters.

To give one more importance of phylogenetics as tools to studies of functions and history (and of adaptation) is the matter of convergence. Very briefly, phylogenetics can give us evidence that dealing with homoplasy, i.e. structures that look similar but that are not inherited from a common ancestor (McGhee, 2011). Further, within the phylogenetic tree, can even tell us if we are dealing with parallelism or convergence. Thus, according to Scotland (2011) there are some criteria for determining if a homoplastic trait is a convergence or parallelism: (1) Homoplastic phenotypes in closely related taxa represent parallelism, while in distantly related taxa represent convergence; (2) Homoplastic phenotypes have the same ancestral character states for parallelism but different ancestral character states for convergence. Besides, he adds one extra phylogenetic criterion: (3) Parallelism comprises homoplastic phenotypes caused by the same underlying genetics resulting from an ancestral predisposition to evolve the same character states, whereas convergent phenotypes are caused by dissimilar genetics. However, with the evidence (1) and (2) we can have well-supported hypotheses of convergence. Convergent evolution played one important evidential role in adaptationist thinking. Using the old adaptationist thinking they reached some ideas as the following: "What else but natural selection to minimize the energetic cost of high-speed travel through water could explain the similarities among these marine predators? Why else would this trait have evolved repeatedly under these particular environmental demands?" (Sterenly & Griffths, 1999). Convergence, in some cases, can serve as evidence for an adaptationist hypothesis (see Losos, 2011). Nevertheless, as showed, without a proper phylogenetic tree, it is not even possible to tell, reliability, whether something is a convergence. Only after this evaluation that we can begin to determine if natural selection was the factor that performed this character modification.

Therefore, those new analytical tools that gave the proper names: "The New Adaptationism" by Rose & Lauder (1996) or the "Adaptive-historical thinking" by Griffiths (1996). As Sterenly & Griffths (1999: 244) affirmed: "The comparative method is one of biology's main windows on the past.” Now we can go back to Rose & Lauder’s (1996) three directions to a “post-spandrel” evolutionary biology. Before I scrutinize the use of (1) phylogenies with its problems and the relations to functions (3) in the comparative method, we should critically exam the use of (2) population biology in this adaptation and functions analysis debate in the light of the discussions of the historical sciences (see table 1) given earlier.

10.4. Population genetics and adaptations

Another instance of misconceptions about the conflations of historical and experimental in evolutionary studies is in relation to adaptation. What is adaptation and what evidence can we seek in order to confirm if a trait is an adaptation? Although very central to evolutionary biology, biologists and philosophers alike are troubled by the definitions of adaptation. One widely discussed concept is the one that considers adaptations as traits that contribute to the fitness of organisms, and others that considers adaptation as selected functions (Sterenly and Griffths 1999). West-Eberhard (1992) erected some criteria as confirmational evidence of a trait being an adaptation: 1) the same form or similar forms (same design) that occurs in similar environments in unrelated species (specially due to convergence); 2) for some characters in a particular context, in which their components can be related mechanically to some particular function in that context (the goodness of “design"); 3) from altering a character experimentally (or eliminated), in order to see how this affects its efficiency in a particular function or environmental condition (a modification of 2) and 4) the efficiency or reproductive success of different forms within a species are compared in the situation(s) where they are hypothesized to function as adaptations. Finally, today it is widely recognized that all these evidences are a matter of proportion: some traits are clearly adaptations, while others are not (Griffiths 1992). The issue is what process was imperative for the evolution of some peculiar trait; for instance, which, of these four factors, or a mutually combination of them, acts as evidence of adaption.

The influence of population-genetic theory in the study of adaptation increased at high rates during the last decades. In their authoritative book on methods of adaptation, Orzack and Sober (2001) argued that although the “molecular revolution” in biology had important implications for the test of adaptationism, they still relate to nonmolecular traits because the focus in evolutionary biology has traditionally been on behavioral and morphological traits. Later they (Orzack and Sober 2001, p. 14) reach a, very important, conclusion: that although

DNA can be very helpful for adaptation, they are very problematic in relation to functions because: “[T]he functional consequences of nucleotide substitutions can be difficult to determine.” Of course, population geneticists can, and indeed did, great contributions to these studies, because of the simplicity of trait definition (nucleotides) and the precise assessment of the role of natural selection and drift (neutral models) in evolution.

Armed with the constructs of the preceding section I shall give one bona fine example of a populational study of adaptation from James et al. (2016); these authors expected that populations of species living on islands would have low effective population sizes, low levels of genetic diversity and less efficient selection. For that, they followed the premise that low diversity and low Ne could reduce the adaptive potential of a species, because the level of available alleles available for evolution to act upon are low as well. In addition, these populations are expected to have inefficient selection (tendency to fix deleterious mutations). In their experiment, they took mitochondrial and nuclear sequences from birds, reptiles, amphibian, mammal, invertebrates, and chloroplast sequences for plants. These sequences where used to calculate the rates of nucleotide substitution: if the diversity of substitutions was different but specifying the same amino acid (synonymous substitution) or if the substitutions was different but specifying a different amino acid (non-synonymous substitution). Posteriorly, they used these data to test for differences in levels of adaptive evolution between island and mainland species so that (James et al. 2016, p. 1879): “Positive values indicate that the dynamics of evolution are dominated by positive selection and negative values that slightly deleterious mutations predominate.”

At first, as expected (confirmed initial hypotheses by expected by the prediction), they found that in some islands the species presented significantly lower synonymous diversity; the authors attributed this pattern to a subset of island species that had a recent population bottleneck (because they are likely to have been founded by a small number of individuals). But in other islands, the authors found little difference in the Ne between a species on the island and in the mainland. In these islands, they also found weak evidence that selection is less efficient to the researched species. Finally, they also found no significant difference in non-synonymous substitution; if found high, could account for high rates of adaptive evolution. What could explain these surprisingly results? They brought up some potential explanations for this: if these island species are founded by multiple individuals, they might inherit much of the variation of the mainland species (but they have no evidence of this however); or island colonization has no lasting impact on molecular evolution.

What is important to note here is the notion of adaptation, as it is notable non-historical in nature. Because they are restricting the concept of adaptation as substitution on DNA, they are able make predictions: if adaptation is occurring, then a significant amount of non-synonymous substitution will be found. The history of the character or the taxa is viewed, thereby at least, as non-essential. This is a clear and direct test of their observation. Their emphasis was on predictions (whether positive or negative), and their evidence remains intact (able to repeat this experiment on the same taxa). Finally, statistics (significant tests and bootstrap) were used throughout their paper for consistency and to avoid errors (as resumed at table 1). What could be the explanation for these significant non-synonymous substitutions? If different, what could account for the existence of these differences? What are the functions of these data? As Erwin (2009, p. 188) said: “Population genetics, like statistical physics, lacks an historical dimension. In other words, the properties of the objects of study do not change over time.” Thus, we can be able to evaluate the claims of some authors that, as discussed above, argue that an appropriate study of adaptation and the role of natural selection, must rest on the knowledge of the differential survival and reproduction in populations by using information like genetic drift, migration, or recent alterations in the environment (e.g., Wenzel and Carpenter 1994, Reeve and Sherman 2001, Grandcolas 2015). And it must be plain to see that the epistemological restrictions that are available in these hypotheses make the same assumptions between the distinctions of microevolution and microevolution. Therefore, to ask as a desideratum of a hypotheses of adaptation information about the underlying basic tenets of genetics and population biology, that can only be studied directly among extant taxa, is to conflate historical and experimental sciences. As it is known, the historical record of evolution comes, in various cases, from fossils and phylogenies, and their observations can only be reached by inferring indirectly from the patterns of characters distributed among lineages.

Thereby when evolutionists demand that for a “complete” study of adaptation both phylogenetic and populational studies must be included (e.g., Grandcolas 2015; Leroi et al. 1994), they are demanding more than that each field can give. Only when we have avoided the problem of the conflation of the differences sciences that we can see that the phylogenetic and the population studies are complementary (Larson and Losos 1996) but independent in their evidential and confirmatory claims. Considering the methodology of the historical sciences (e.g., Cleland 2002, 2009), this is exactly the kind of misconception that the experimental minded scientist commits when the methodological differences are not fully appreciated. In conclusion, one can argue with confidence that the origin of a character, for instance, the acquisition of jaws in gnathostomata as a major key innovation in vertebrates (leading them to radiate into every conceivable habitat), allowed them to acquire new functions, e.g., to capture and utilize an extraordinary range of prey as food (Hall 1999), is an adaptation even though population studies were not necessary for the confirmation of this ascription.

11. Systematics and Evolution

11.1. An overcame first disillusion

All systematic methods use data that have resulted from evolution.

Farris (2011: 217)

After having exposed how to avoid the failure to conflate these different sciences, I will show how it was, (and still is for some cladists), the relation between evolution and systematics. It is commonplace in evolutionary biology that the study of adaptation it is within its core. In addition, natural selection, the explanation of adaptation, is also the primary, but not the only, force for evolutionary change. In this section, we shall see how the matters of functions and adaptations have worked in Phylogenetic Systematics. Earlier in this researche group, Hennig (1966: 217) already demonstrated the importance of adaptation for systematics by stating that: "The problem of adaptation, which deals with the relationship between development of form and the environment, is one of the basic problems of phylogenetics, and special systematics must contribute to its solution." Hence, it is plain to see the preoccupation of Hennig in conducting phylogenetic research with adaptationist considerations, although the theme of adaptation appears very rarely in his book, it is relevant to the "causal relationship" between taxa.

However, some cladistics choose to decouple systematics from evolutionary theory (Brady, 1985; see also Platnick, 1979; Brower, 2000; Williams and Ebach, 2008), and this movement was branded ''pattern cladism'' by Beatty (1982; see also Hull, 1988), even though initially (Platnick, 1979) they intended to call this "speciation" (Hull, 1988), or early cladogenesis (Rieppel, 2014), of cladistics as transformed cladistics[12]. The arguments by the pattern cladistics can be resumed by the following argument (Platnick, 1979: 539): "So if

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[12] However, Farris (2014) preferred to call them as "pattern taxonomists", in a criticism to their separation of evolution in methodology, as cladists (correctly) does not make this separation, those "transformed" cladists should not be called cladists.

classifications (that is, our knowledge of patterns) are ever to provide an adequate test of theories of evolutionary process, their construction must be independent of any particular theory of process.” Thus, patterns of characters, in the form of a hierarchal order in nature, are sufficient to determine the cladistic relationships. No evolutionary assumptions must be considered in this process, they can be only analyzed after the construction of a cladogram.

Usually, the authors that sympathize with the so-called pattern or transformed cladistics, complain that their ideas are mis-labelled as “theory-free” and “anti-evolutionary” and claim that the literature is full of misconceptions and confusions. Even claims of, what Williams & Ebach (2014) termed, “auto-editing,” the procedure of (Williams & Ebach (2014: 174): “…editing out the apocryphal literature from a politically motivated (and usually false) message…” The history of the patterns cladists was told, retold and told one more time in a number of publications (e.g., Hull 1988; Williams & Ebach, 2008; Rieppel, 2014; Nelson, 2014), with different views and a particular agenda behind for each one of them. Within their history, Rieppel (2014) identified Ronald H. Brady as the one responsible to formulate the basis that constitutes the historical and philosophical foundation of pattern cladism. This view is confirmed by the recent publication of the paper “Ronald Brady and the cladists” by Malte Ebach and David Williams (Ebach & Williams, 2019), in which they provided an overview of Brady’s contribution to (pattern) cladists (ending this paper by urging other systematists that his work should not be forgotten). Brady published a series of articles defending the pattern cladistics (Brady, 1982, 1983, 1985, 1994a, 1994b), but I will take his 1985’s article “On the Independence of Systematics” (Brady, 1985) for discussion, as it is the one that resumes his main ideas, and for being “…perhaps the most elegantly developed argument for the “independence” of systematics” (Schuh & Brower, 2009: 47). On what follows, I will scrutinize his arguments from a philosophical and ontological point of view.

11.2. Brady’s independence of evolution

Brady (1985) begins his argumentation by describing the error to make a reference to evolutionary processes in systematics and, referring to Ernst Mayr, the worst mistake is to consider classifications as records of evolutionary inferences, or, in other words, he accuses Mayr to conflate pattern with process (*explanandum* with *explanans; sensu* pattern cladists). Later, Brady (1985) uses the strategy “to throw the mantle of the great Darwin” (Hull, 1988:

202) to his own shoulder. Heavying citing Darwin (1859) thought out the paper, he tried to show that he interpret Darwin correctly, and that he was, in some way, more "Darwinian" than his colleagues. Let us now see how his arguments works.

Darwin developed an explanation of why taxa exhibit an order in nature (same pattern; same relative position); he used his theory of natural selection for this explanation. Thus, homology can be explained as a confirmed test evidence for Darwin's theory of common descent (or his "propinquity of descent"). As it is known by philosophers of science, theories must be compared in order to appreciate the correctness or faulty in one's theory. Thus, Darwin compared his "descent with modification", in order to show that his theory was a better explanation for the "order in nature". What was his rival theories? Darwin struggled, mainly, with the possibility for "the Creator" to explain this pattern between species, or a "…independent creation of each being…" (Darwin, 1859: 435). Thus, only supernatural design can explain the order in the nature and the structures of each organisms as complex adaptations. This is the "argument from design", a popular argument made by defenders of natural theology, i.e., the existence of each pattern was designed by its creator (God). The main problem with this argument is that it can explain anything (any kind of outcome), at the same time it can not predict anything (Sober, 2008) because any pattern can be explained equally well (it does not prohibit anything). Facing different interpretations for the same evidence, homology as common descent was not something given, it must be supported by evidential claims found in the way of the sameness of form. Likewise, Darwin wrote (1859: 206) that "On my theory, unity of type is explained by unity of descen", thus it mean that his theory of evolution (descent with modification) provides a mechanism (in the form of what kinds of entities and processes happens in an evolutionary explanation) in which a causal explanation can be made for a particular homology.

To say that a particular trait exists in particular taxa due to "descent with modification" does not give us a causal explanation. For instance, why does the zebras have stripes? To answer this question by stating that is due to "descent with modification" does no give us any causal explanation at all. However, when we can give a functional explanation for this trait - zebras use their stripes to ward off biting flies (Caro *et al.*, 2014) - we are able to give a causal explanation. But, very importantly, this was due to Zebras in the past, had those stripes, that were inherited from its ancestor (Darwin's theory of common descent; populations as part of an ancestor-descendant history) that, in this way, was maintained by its extant members. Thus, natural selection won't solve the explanatory riddle of functions and causality by itself.

The explanatory framework of “descent with modification” was already incorporated in the causal explanation for the Zebra’s stripes, in other words, the background knowledge required to draw testable consequences from a theory was already included in this single causal explanation. We can consider this background knowledge because it includes the relevant experimental results, theory and consequences that this theory contains. Thus, if we consider “descent with modification” as a background knowledge, as most evolutionary biologists do, the theory of common descent is already considered as given, and we construct your new causal theories within this framework. Hence, we do not need to test if the presence of stripes in zebras is a confirmation of the evolutionary biology in relation for being homologous; we do not need to test it against the “argument from design” as the natural theologists would do, as this option became unplausible after 1859.

As Brady (1985) argued, for Darwin, the pattern of traits found in the organisms would be the fact to be explained, and his theory of common descent would be the explanation. Darwin (1859) was at great length to explain why his theory is the only plausible answer to this evidence. So far, so good. However, this is true for pre-evolutionary times; after Darwin’s theory, and the posterior developments, e.g., the Modern Synthesis, his theory was widely accepted as our best current evolutionary theorizing. In this way, we could advance our studies and need not to be concerned if traits and patterns were a result of “intelligent design” or “descent with modification.”

The whole issue with Brady’s argument is notorious when he applies this temporal logic to contemporaneous evolutionary biology. For instance, he wrote (Brady, 1985: 116): “…given that our hypothesis of process was designed to explain how that pattern came about, it would seem that the pattern must be taken as factual before we produce a hypothesis to explain it.” Of course, I, and most evolutionary biologists, would agree with this statement, if, and only if, it was restrict temporally to the years before 1859. When Brady extent this argument to contemporary evolution, he is making a temporal mistake. Furthermore, Brady complains that Mayr suggestion that the patterns (homology) of systematics should be based upon the theory, or in other words the pattern of groups defined by synapomorphies, must be discovered prior to the application of evolutionary theory and must be defined independent of descent with modification. Brady further elaborate unto these arguments, and, for the sake of clarification, I will show the full quotation: “We must still advance an account of the empirical conditions to be explained-we still need a name for the relation of identity (common position in a common plan) found within the data. If we fail to supply this, we fail to distinguish empirical problem from explanatory hypothesis, and once this has happened, *we have no independent evidence with which to test, or support, that hypothesis*. By making our explanation into the definition of the condition to be explained, we express not scientific hypothesis but belief. *We are so convinced that our explanation is true that we no longer see any need to distinguish it from the situation we were trying to explain*. Dogmatic endeavors of this kind must eventually leave the realm of science (my emphasis)".

There are two mains claims in Brady's argument, and I shall discuss them now. The first matter brought up by Brady is related to the 'Fallacy of Circular Reasoning', that is plainly, when the accuracy of the conclusion is already assumed in the premises that support that conclusion, in other words, the accuracy of the conclusion is presupposed when justifying the premises. Thus, for Brady and other pattern cladists, this would be the greatest failure of the "traditional" (transformational) cladists, as they incorporate and justify its methods by using evolution as background knowledge. The first thing we need to discuss in explanation and confirmation, is mainly related to the component of a Popperian hypothetico-deductive approach. Before differentiating them, let us see the following argument provided by Brower (2019: 12): "…according to Popper (1979: 350-351), "the *explicandum* is definitely known to us - the fact lies before us in stark reality. If we want to explain it, we must try out some conjectural hypothetical explanations (as the authors of detective stories do); that is to say, explanations which introduce something *unknown*, or at any rate much less known to us." Under such circumstances, "descent, with modification" takes the form of the universal law in the premise."

These quotes refer to the "dead rat" example, given by Popper (1979: 350-351). Put simply, Popper asks for an explanation for the appearance of a dead rat and gives us the initial condition that "This rat has eaten some bait containing a large dose of rat poison". Afterwards, Popper give us the following "universal law"[13]: "If a rat eats at least eight grains of rat poison it will die within five minutes." From this, he claims that we had fulfilled a scientific explanation based on the Deductive-Nomological model. The following scheme can be taken from this example:

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[13] This is clearly not a universal law; however, for the sake of Popper's example, I shall consider it as it would be one.

Explanans: initial condition: 'This rat has eaten some bait containing a large dose of rat poison'

universal law: 'If a rat eats at least eight grains of rat poison it will die within five minutes.'

____ logical deduction

Explanandum: "This rat here died recently".

This is clearly a valid logical deduction, however, we are missing something in the initial condition, for instance, if the rat really died from food poison. Thus, if this is the case, then his digestive tract must have some poison as pointed by Popper. Accordingly, your *explanans* was not completely confirmed. If it was the case that the digestive tract of the rat did not have any poison trace (or any other test evidence to confirm that the ray dead of food poison), our initial condition 'This rat has eaten some bait containing a large dose of rat poison' would be false. The straightforward conclusions is that before we try to explain an event we have to establish that the event actually did take place. Therefore, we are dealing with the confirmation of observational hypothesis and not with explanations. This is the famous hypothetico-deductive schema for scientific confirmation, or for Popper, falsifiability. If our initial condition is false, our *explanadum* is false, even though it is a valid deduction. This is the reason why Hempel (1965) proposed the empirical condition of the *explanans;* that has to be highly confirmed by all the relevant evidence available (besides for being testable), because if our initial condition is false, we will fall into serious problems. Clearly, Popper did not make that with the initial condition because we have an unconfirmed statement in relation to the poison ingestion by the rat. Of course, if we are testing the hypothesis that this particular rat ate the poison, it would not be illuminating to use it as a premise to the statement 'This rat has eaten some bait containing a large dose of rat poison'; it would be viciously circular. If we are testing this hypothesis, we need to search for the evidence elsewhere; for instance, test if the poison is present in the rat blood, to look for the poison at the digestive tract, etc. As Salmon (1989) put it, in a Deductive-Nomological model we must use only well-confirmed scientific hypotheses, laws, or theories in the *explanans,* this is so because the function of the explanation is not to support the truth of its conclusion (the *explanandum*), as that is already presupposed when we used it for given us the explanation. However, the hypothetico-deductive method, in contrast, is used to provide evidential support for a hypothesis (the *explanans*) whose truth (or correctness) is being questioned.

Now, it must be simple to see that those problems pointed by Popper and Brady are pseudo-problems. Thus, considering a Deductive-Nomological model, even if we used “descent, with modification” as a premise (*explicans*) forming the universal law (for the sake of the argument, let us assume that it is a universal law), using it to explain a homology (or synapomorphy) **is not circular**. We are just using our best theory (well confirmed) of evolution to make your explanation; this is exactly what a scientific explanation must have in order to give us genuine explanations. As a matter of example, even if it does not works as a genuine scientific explanation accordable to Hempel and Popper (for the reasons of functional equivalence, the historical propriety of systematics, along with other factors), let us propose a Deductive-Nomological scheme for the explanation of homology:

Explanans:	universal law	Evolution as Such[14]
		Evolution by Common Descent
		Gradualness of Evolution
		Natural Selection
		Multiplication of Species
	initial condition	Sameness of a particular trait
________________________________		parsimony (congruence of characters)
Explanandum:		Homology (plesiomorphy; apomorphy) or
		Homoplasy (parallelism; convergence)

As common descent is already well confirmed, it can be used as a general law to deduce as *explanadum* the explanation of homology (as it can do with homoplasy). Complying with the fact that we are not testing common descent because we already accepted descent with modification as a well-confirmed set of hypotheses, it is not circular while inferring homology.

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[14] Based on Mayr (1982)

The argument for the independence of systematics that links the problem of circularity of explanation with the thing to be explained is not very cogent. Thus, the points made by Brower (2019: 13), can be very problematic: "Because it makes no *a priori* assumptions about mechanisms of evolution, pattern cladistics provides independent evidence supporting the theory of evolution, which legitimates and frees from circularity the explanation for the patterns systematists observe." If, however, pattern cladists were proposing an alternative to the theory of Darwin, them, surely, it would be problematic to use "descent with modification" in order to test this same theory. But this is clearly not the case as no cladist, pattern cladistics either, deny the content and implications of evolutionary theory, as the following quote shows us (Brower, 2019: 5): "…pattern cladists have never asserted that evolution is not a well-supported empirical theory…"

The other point by Brady is that it is "dogmatic" that we are convinced that your explanation is true and "do not distinguish it from the situation we were trying to explain". This point is made again in other place (Brady, 1985: 125): "If we lose the distinction between the detection of pattern and its explanation by a process hypothesis, we lose the reason for our inquiry, not merely historically, but logically." As a corollary of these arguments, Brady (1985) concluded that synapomorphies are prior and independent of evolutionary theory. Accordingly, the whole concept of an evolutionary transformational series (Grant & Kluge, 2004), as put it by Hennig (1966: 93): "'Transformation' naturally refers to real historical processes of evolution…", would not deserve it is "evolutionary" conception, mainly because it could be only interpreted in a purely empirical sense as a pattern within patterns (Nelson and Platnick, 1981). As a response to Brady's question (1985: 124): "That these patterns can be worked out without reference to evolutionary theory is not contestable. The only question resides in the advantage or disadvantage of doing so."; I would answer that this is not just a disadvantage, but it is impossible, even in principle. Homology must be studied with the evolutionary process in mind, the two-step approach - taxi (pattern) and then transformations (evolutionary) homology is rejected, as it happens to over evolutionary studies (see, for instance, Mahler *et al* 2017). Cladists cannot wipe their minds clean to process theories, and even if they could, it would unwise to do so.

One question remains to be answered: what is, then, the relation between homology and evolution? As it was argued, "descent with modification" is within our web of theories that compose our knowledge of the world. As Quine (1951: 42) claimed: "…the unit of empirical significance is the whole of science.", thus when we aim to test some hypothesis, other hypothesis assumptions are taken as well-confirmed, and we do not aim to test it again and again; we take it as confirmed (but not proven) wholes. For instance, we do not challenge the law of gravity, our theories of hereditarily, or our geological theories of the dilatation of time when we are inferring phylogenetic relationships; however, they are included in our hypothesis (whether we are aware of that or not). Thus homology assumptions, as the ones claimed in a phylogenetic hypothesis, does not need to take it as evidence for evolution as argued by Wake (2003), instead, the evolution as a 'fact' is followed (*sensu* Mayr, 1982) and as a well-confirmed theory that is part of your background knowledge, homology can be considered as the 'anticipated and expected consequence' (Wake, 1999) of common ancestry. Thus, phylogeny, or homology, cannot be "the real test of evolution" (Ridley, 1986) - is there a "real" test? Therefore, when we study homology, we study evolution, or better, the effects of a complex history of traits that are subject to selection processes and constraints.

11.3. Patterns and explanations

I have discussed that the conceptual problem between explanation and confirmation can be very problematic, leaving some erroneous interpretation of circularity. Indeed, the issue of explanation in science as elaborated by Williams & Ebach (2009) is a very peculiar one, and it deserves some brief discussion. Williams & Ebach (2009), at first, discuss that an explanation of particular, or singular causal, explanation is an inference either to the unknown or unknowable. If it is unknowable, how they expect to have an explanation? What is an unknowable explanation? However, the authors do not develop this line of reasoning any further. Indeed, it remains a very peculiar approach to explanation. One thing is certain, citing a nonevent (unknown) to explain another nonevent (unknowable), is counter-intuitive, fallaciously and inconsistent. The things are even worst when Williams & Ebach (2009: 250) claims the following: "An explanation is the epistemic equivalent of an excuse—any data can be made to conform to any explanation. An explanation is chosen relative to its rationality, or its plausibility." The only possible consequence of explanations ta can be "made to conform to any explanation" is the natural theology; any pattern (or explanation) is possible, even the wings of angels. Indeed, this reasoning is absurd, and it is difficult to follow their view, because in doing so we must simply forget everything that was developed about explanation since Hume's time; as scientific explanation (even the one developed by Popper) is a rigorously and logical impeccable construction, that does not permit "an epistemic excuse". Later, Williams

& Ebach (2009: 250) claims that explanations are “immune to empirical endeavour”, mainly in the historical sciences. As I have been arguing along this essay, most explanations are causal explanation, and we explain an event by citing its cause. Another characteristic that was completely ignored by those authors, is that all models of explanation is physicalist in their argumentation, i.e., they all attribute some mind-independent empirical feature to causation - testable (in potential) evidential information - which a causal explanation has to grasp in order to have an explanation after all. Indeed, all explanations (causal or not) have empirical claims that can be tested by observations by our test evidence. Therefore, explanations, as a cognitive understanding of our scientific image, are **not** “immune to empirical endeavour”, actually, it is deeply dependent to empirical tests to have an access to ontology.

The other cladists[15], the ones that accepted evolution, were entitled as Hennigian phylogenetics. Today it is common place to consider, and justify, cladistics by evolution, therefore when I refer to cladists, I will mean those who consider evolution as a background knowledge. Now, we shall see how function and adaptation were considered by systematics.

11.4. Homoplasy as a process: an optimistic view on the recurrence of evolution

Wing of bats and birds are, after all, convergent as wings, but homologous as forearms.

Gould (2002: 1079)

Cladists have traditionally view homoplasy as a problem. Sometimes as an error (“error in homology assessment"), sometimes as an *ad hoc* hypothesis. The main argument is that homoplasy is always misleading evidence that produces wrongly relationships, or at least making the delineation of phylogenetic relationships difficult. I will review these arguments in order to see if homoplasy is really so problematic and if it really “exists” in nature. I will focus on the arguments made by Carpenter & Nixon (2011) and Farris (1983, 2008), as these

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[15] In the literature, we can observe that the name "cladist" appears replacing "phylogenetic systematics" derives from Mayr (1965). He used cladistics to refer to the persistence of this research group in merely reconstructing the "branching pattern". He believed it was misleading that cladists call themselves a phylogenetic school, for they would ignore much of the phylogenetic process, e.g. ignoring differences in evolutionary rates (grades). This terminology, even if initially despised by the cladists (Hull, 1988), has been adopted by the systematists, and, therefore, will be used interchangeably herein.

arguments and justifications are the ones most used by cladists who accepts this line of reasoning.

In order to make their argumentation that homoplasy would be an error, Nixon & Carpenter (2011) tried to attribute some instances as a matter of analogy and convergence. For that, they defined these concepts as follows: convergence would be a functional similarity, but not genetic one; analogy would be similarity in function, without the necessary similarity of form (development). The problem here is that both definitions possess the phrase “similarity in function”. Thus, they are conflating the meaning of analogy and convergence (a case of homoplasy). Although the concept of analogy as convergence (Stayton, 2015) lacks consistency in relation to definitions, I will follow the usual description as similarity due to the similar function (Lankester, 1870; Haas & Simpson, 1946; Cracaft, 1967). On the other hand, convergence is not essentially **only** due to a necessity of functional similarity, but essentially is similarity that is not due to common ancestry (between the taxa being analyzed), so that it occurs in distantly related taxa with different ancestral character states and by a dissimilar underlying genetics mechanism and development (Scotland, 2011). Hence, function does not constitute a criterion for convergence. So, for instance, a case for similarity due to convergence in form and not the function can happen in cases when some trait is a correlated response to selection on another trait or for a pure chance (Losos, 2011). When can, them, restrict analogy as superficial similarity that arises through functional reasons, usually by convergence. In other words, analogy can imply a common selected function as the underlying basis for a similarity (Powell, 2007). Hence, analogy can be seen as a potential (if untested) explanation for some cases of convergence. Analogy, as homology, can be explanations of perceived similarities. In order to make these inferences, we need first to state if these similarities are due to homoplasy, or if they are homologous. Then, we need to make a claim for analogy only after a phylogenetic analyst has been made. If it was shown that it was the case of homoplasy (convergence), then we need to show this was due to analogy.

Nixon & Carpenter (2011) make the assumption that we would not consider wings of birds and of insects as homologous; however, we neither could make the conclusion that it is a case dealing with homoplasy. So they considers analogy as the third option, because there is no similarity at all. However, as we have seen, analogy is a potential explanation of homoplasy (convergence), then there is a similarity (even if not homologous) among wings of insects and birds, and this happens because they have a continuity of form (similar design) due to the engineering constraints required to fly (same aerodynamical function).

By pointing that the wing of birds and insects and the bill of the (mammalian) platypus and the bill of birds are cases of neither homology or homoplasy, but instead of analogy, they concluded that (Nixon & Carpenter, 2011: 164): "…*homoplasy is merely a conclusion that we were in error when we hypothesized two conditions to be homologous*." However, even if we do not score the wings of birds and insects and the same character state, we could still have other evidence that these structures are similar (similar design) due to convergence of function. There is plenty of evidence, beyond the phylogenetic tree, that confirms this view. When we are in face of no so obvious case of convergence (or homology), we surely must score the characters in order to have evidence for homoplasy or homology. If they are homoplastic (or homologous) we can establish a framework for a future test that can give us a confirmation that it is indeed this case as obtained at the phylogenetic tree. Further, we can establish the function of that particular trait; if we can give a common function (or analogy) for those similar traits that appeared independently in two taxa that are not related, we can assert that the presence of the same particular function evolved in order to survive at the similar selective environments or selective process (adaptation has happened).

Is homoplasy an error of homology? If homology is the presence of trait due to common descent, thus homoplasy must **always** be a case of descent that is not due to common descent. Let us take the well-known example of wings in insects. Within the Insecta, the group called Pterygota comprises the winged insects. Practically all this insect possesses wings, but the group composed of fleas, the order Siphonaptera are wingless insects. As the fleas are ectoparasites of mammals and birds, they retained some typical traits related to this habit, the losing of wings being one of them. As it has been traditionally considered (e.g., Hennig, 1981; Kristensen, 1991), absence of wings is autapomorphic in fleas, even though it is homoplastic in relation to the entognathan hexapods, Collembola, Protura and Diplura, that are plesiomorphic wingless. So, in this case, we should call this absence of wings in fleas as "an error"? Or as a homoplastic trait that is due to specialization to the ectoparasite life? Surely, no one would say that this an error, but as an effect of the process that fleas are adapted for (ectoparasite life). Thus, within the clade of the Siphonaptera, this homoplastic trait is due to common descent, and all flies are united by this trait. However, if we see it more globally, i.e., the entirely phylogenetic tree of hexapods, this trait is only a matter of homoplasy that is not due to common descent. Hence, when more characters are added fleas are not sister group with entognathan hexapods. This example was clearly seen in the phylogeny of Wheeler et al. (2001), which inferred the relationship of the extant Hexapod orders, and scored wings as synapomorphic to Pterygota, but as homoplastic (reversion) in Siphonaptera. Whit this example, I tried to show that the received view in cladistics that all homoplasy is misleading, does not hold (Wilkinson, 1991; Assis, 2009; Franz, 2005). As Wilkinson (1991) argued, homoplasy in taxa that are sister group can be evidence of phylogenetic proximity as this trait evolved in the ancestor of these lineages. Thus, some homoplastic traits can be a reliable evidence of relationship (Assis, 2017).

There is a hierarchical correlation to homoplasy in a way that in some levels it can be informative about relationships as shown, but sometimes it can be indeed similarity due to chance (stochastic evolution) or developmental constrains (Stayton, 2015); and this trait is not reliable evidence of common ancestry, being misleading evidence. This matter results from the principle that the history of the true phylogeny is never known, and transformations character evolution, with a contingent and complex history, depends on the various evolutionary assumptions and process. Only then we can have a reasonable inference about sister group relation with its traits being a reliable source of evidence (as it is the source of evidence of cladistics). Homoplasy, homology and functional assertions are inferences on the evolutionary process, and are not easily testable, mainly because phylogenetic claims are all about the past, and the relevant evidence may have been forever lost. Thus, some hypotheses may remain forever untested. However, sometimes the tests can be reliably done.

Take following well-knows example of adaptive radiation of cichlid fishes in the lakes of East Africa (Kocher *et al.*, 1993; Ruber & Adams, 2001). These fishes, derived from different lakes, has a highly similar form of tooth shape and body shape. Phylogenetic analysis showed that these fishes acquired these similar traits independently, so that they are homoplastic, in this case, convergent traits. Is this merely an error? Is there no process that could explain these similarities that are not due to common ancestry? Various author suggested that natural selection is the driving force in the evolution of convergent forms in this case. Ruber & Adams (2001) pointed that trophic ecology, as multiple specialization times in independent lineages, explained these similarities. These trophic niches thereby facilitated ecological segregation, and drove independent invasions of the same adaptive zone.

With all this background, we have the weapons to analyze how Nixon & Carpenter (2011) develop further their criticism of homoplasy; they affirmed that (Nixon & Carpenter, 2011: 164): "*…homoplasy is error in our preliminary assignment of homology* while scoring the character matrix." Thus, for then, this "error" could be correct only by (Nixon & Carpenter, 2011: 164): "…rescoring the matrix such that the homoplastic states are considered to be states of separate characters, at which point they are analogies, not homoplasy." And finally, they end their argument by stating that (Nixon & Carpenter, 2011: 168): "…difficult or rapidly evolving characters are not ‘‘prone to homoplasy’’—they may be prone to high rates of mutation or to high levels of convergence, but it is we who are prone to homoplasy, since we are the source of the character codings that imply homologies that are not supported in the results of our analyses." The contradictory statement is clearly found when they state that convergence can be considered as a process and an explanation for homoplasy, while homoplasy by itself is an error, and "does not exist" (Nixon & Carpenter, 2011: 164). If convergence is similarity (ontological similarity) that can be discovered by our phylogenetic analysis as homoplasy (for definition, convergence is similarity not due to common ancestry), how could convergence exist? If homoplasy is an error, and could not exist, convergence is an error that cannot exist as well. If it was a case of self-indulge and careless scoring of traits, it should be plain to see that the similarity due to convergence, and not homology, of the cichlid fishes in the lakes of East Africa is one more case of error and nonexistence. Of course, homoplasy could be an error of scoring the character and character states, for that we can check and recheck these same characters to try to understand if this was the case of a mistake. However, this is the same case of homology, we always can make mistakes when scoring traits. Nevertheless, Nixon & Carpenter (2011) considers homology as a real and ‘existent’ process. These authors put homoplasy on a lower epistemological level than homology. Only homology exists and can recognized as a process, so there is an epistemic asymmetry between them. These authors created this asymmetry to claim that homology ought to be preferred as our only explanation of genealogy, that homoplasy does not hold ontologically (all similarities not due to homology are mistakes; it do not exist outside our cladogram). I do not think this asymmetry holds in numerous cases; there are real cases of convergences and parallelism. Let us take as an instance, the study made by Jaekel & Wake (2007). They studied the repeated evolution (in this case parallelism) of the interdigital webbing in tropical salamanders of the genus Bolitoglossa, resulted in two conclusions: that webbing is an adaptation for climbing for only a single species, and for the remaining species webbing does not improve attachment and have evolved alongside other traits, as side effects of pedomorphic tendencies. If Jaekel & Wake (2007) had not considered this repeated similarity as not an error, but as ‘existent’ similarity, they could not have concluded that this parallelism, in most species, is a case of side effects of other traits. I hope I was clear as to have shown how pernicious this "cladistics view of homology as error" can result by insisting in their argumentation.

Later, Nixon & Carpenter (2011: 164) affirmed that: "*homoplasy as process* to be flawed and logically inconsistent… in the context of a generalized scientific method of hypothesis testing." Thus, homoplasy as a process would be flawed in relation to the "generalized scientific method of hypothesis testing." The authors are not clear about what a "generalized scientific method of hypothesis testing" is. However, as mainstream cladists, very probably, they are talking about hypothetico-deductive (H-D) scheme of scientific confirmation based on the Popper's falsificationism. Briefly, it holds that when a hypothesis has undergone severe tests, and if the predicted facts fail to obtain, we reject the hypothesis as falsified (method of conjecture and refutation); if not refuted, this hypothesis is corroborated (Popper, 1959). Popperian method along with his H-D model has been widely criticized by a number of authors (e.g., Salmon 1967, 1989; Lakatos 1970; Kuhn 1970; Feyerabend, 1975; Laudan 1986; Sober 1988, 2008; Mayo 1996; Stamos 1996; Cleland 2009) which indicated philosophical problems and paradoxes; and one of the main argument against it is related to the Quine-Duhem thesis (theoretical and background assumptions play integral roles in the rejection of hypotheses). Even within a flawed methodology of Popper's falsificationism, homoplasy would still count as a genuine hypothesis, being testable and not a metaphysical research programme. In a scheme more aligned with how hypotheses are really dealt, homoplasy is testable and can be confirmed or disconfirmed accordingly to its resultant test evidence, as the example of the convergence of the cichlid fishes in the lakes of East Africa showed us.

Finally, the motive for all these strong opinions about homoplasy delivered by Nixon & Carpenter (2011) is demonstrated in their citation of justification of cladistics made by Farris (1983). However, for Farris (1983, 2008) homoplasy is not an error, but instead is a matter of unexplained similarities. However, these homoplasies (or "*ad hoc* hypotheses of homoplasy" *sensu* Farris, 2008) are unexplained in relation to inheritance from a common ancestor. This position is maintained even when the matrix was "corrected" by removing morphological variation and errors of observation. As only homology can be explained by common ancestry, by minimize homoplasy (similarities unexplained), the "explanatory power" of a phylogenetic tree is maximized and are, thus, preferred. There are two problems by this justification: 1) this asymmetry between homoplasy and homology does not hold and 2) there are possible explanations for homoplasy, even if not by common ancestry.

As aforementioned, the Farris' (1983, 2008) asymmetry does not hold and his explanatory power schema fails as well. Sober (1988), arguing that no genealogical hypothesis explains ‘by itself’ any character distribution, whether homoplasy or homology, that in no significant sense genealogical hypotheses are unable to explain the character distributions they imply to be homoplastic. The problem is that genealogical hypotheses may weakly explain homoplastic and homologous characters, both contributing to genealogical explanation. So with this conclusion, the scheme of explanatory power is systematics by Farris (1983) does not hold and it must be discarded. Another line of criticism is the one given by Vogt (2013) who argues, persuasively, that homoplasies are the result of evolution, being part of its background knowledge (the same argument was made herein earlier). Thus, it cannot be characterized as *ad hoc* hypotheses. Therefore, we must deal with homoplasy in its appropriate form: as an explanation, not as an error. Besides, a homoplasy can group some taxa, the matter here is in relation to a hierarchal correlation of characters; some will give signal - synapomorphy - for some clades and others simple will not. As we have seen, there is various explanations to homoplasy (2): analogy, natural selection, chance, constraints, as side effects of correlations with other traits, and, surely, by scoring mistakes. The statement made by Farris (1983, 2008) that, if the perceived similarity in traits are not due to common ancestry, there is no explanation, is in serious problem, because, as the example given for the cichlid fishes and the salamanders show, there is an explanation indeed. As rightful stated by Rieppel (2007), any character transformation in a tree can be (causally) explained in a number of ways. Of course, there still the option he homoplasy is due to erroneous character conceptualization and scoring. Thus, the best method to avoid these mistakes is to look again at the character coding and reevaluate it in order to exclude, from the best of our efforts, until we are certain that the character cannot be further recoded. This is the famous reciprocal illumination (“checking, correcting, and rechecking”) of Hennig (1966), and is still our best way to detect those mistakes.

Today, the optimistic view of homoplasy is much more appreciated by some systematists (e.g., Assis, 2009, 2014; Franz, 2005). Franz (2005: 504) for instance, affirmed that: “Experience indicates that abundant yet informative homoplasy is as necessary as homology for reliable phylogenetic inference.” Thus, in practice homoplasies support the inference of monophyly, since they are apomorphies (Assis, 2017). For instance, in a work that provided a phylogenetic hypothesis for Tachinidae (Diptera) Cerretti *et al*. (2014) used “homoplasious apomorphies” as indicatives of characters states supporting some groups. After being able to identify homoplasy, the search for the evolutionary explanation of them by a mechanistic basis can be stated as the current *desideratum* to phylogenetics. It is very important to link our cladograms to theories and process of character evolution alongside with the function, genetical mechanism, development of particular traits with ecological studies. As a good example of this approach, Wake (2015) has shown that in order to study homoplasy in modes of amphibian reproduction, she developed an intricate framework, that includes physiology, endocrinology, functional genetics, development, ecology and behavior. Indeed, a total evidence approach as argued by Kluge (1989). But, first of all, as it is widely known, we need a reliable phylogeny to state if characters really are homologies or homoplasies, so it is possible to demonstrate the mechanisms that underlie their maintenance and development (Wake, 2015).

After all, what then, is homoplasy? As a resume, we can say that it is “real” and is both a pattern and process; mainly, they are the end results of the phenotypic expression (Wake, 2015). It is not possible to develop a causal explanation to a pattern without a process, in the same way, that it is impossible to search for a mechanism, and process (e.g., if it is an adaptation resulting for natural selection), if we are not sure (unreliable) of the patterns recovered. Hence we have a healthy interdependence of pattern and process in systematics and evolutionary biology. If the arguments and views of homoplasy as used and considered in phylogenetic systematics made by Farris (1983) and Carpenter & Nixon (2011) does not hold, is there a justification of cladistics? Or, in other words, what compels us to identify homology? Willie Hennig already did the argument and justification as early as 1966. His famous “auxiliary principle” holds the view that a shared presence of a feature is first and foremost indicative of common descent, and independent origins of the feature should not be assumed *a priori* (Hennig, 1966). This is the principle of parsimony as showed and widely argued by cladists. Of course, this does not mean that homoplasies are rare (Farris, 1983) or nonexistent. Homoplasy is something that happens in nature (it has ontological reality) and can be rather common in some groups (Brooks & McLennan, 2002). Later, Henning (1966: 121) justified his procedure by stating: “This was based on the conviction that phylogenetic systematics would lose all the ground on which it stands if the presence of apomorphous characters in different species were considered first of all as convergences (or parallelisms) [homoplasy], with proof to the contrary required in each case.” This seems to me a very strong and cogent justification for our use of homology, homoplasy and parsimony. It does not demote the role of the process of evolution in evaluating our results of the transformation of traits, whether homology or homoplasy.

As a conclusion, there is more to systematics and parsimony than just the search for the shortest trees. Of course, this is the epistemological goal of systematics, and what joins every scientist as a cladist (i.e., our shared derived state). However, as explicitly argued by Hennig (1966, 1981), the goal of phylogenetic systematics is the construction of a reliable tree, using as evidence characters that are confirmed as evidence of common ancestry, and can be used for our inferences of monophyly. As trees are used as abstract resumes of many evolutionary events (effects), we must pursue the evolutionary causes for these events in a way to searching for mechanisms, process, and functions, using every biological evidence as possible to support these results. To sum up, let us take the following quote from Minelli (1993: 15-16): "Evolution does not simply mean splitting lineages (cladogenesis, speciation). It also means adaptation, and constraints. When deciding which state is primitive and which is advanced between, say, the absence or presence of wings, we cannot content ourselves with pattern analysis of presences and absences in a character matrix. We also need to know something about the functional value of the wing, when present, and the possible adaptive significance of its absence."

11.5. Against "weighing against homoplasy"

Basically, there are two forms of character weighting: *a priori* weighting that is tree independent, and *a posteriori* weighting that is tree dependent. Similarly, there are two principal methodologies to put a posteriori weighting to work: successive weighting (Farris, 1969) and implied weighting (Goloboff, 1993). These methods use evidence on homoplasy to estimate character reliability, in order words, the degree of fit between a character and the phylogenetic tree (Farris, 1969). The rationale is that characters which have a greater tendency to homoplasy are less reliable. Thus, both relies on the assumption that the characters to be more reliable (homologous) explain the data better. Character weighting multiplies (up-weight), by creating a new data set, some characters that are more consistent in relation to some other characters that as less consistent, in this case, homoplasy (down-weight). Goloboff (1993; Goloboff et al., 2008; see also de Laet, 2015) connects this idea of weighting against homoplasy to the general ideas of Farris (1983) that maintained that homoplasy is an *ad hoc* hypothesis because it cannot be explained by inheritance from a common ancestor. As a result, these procedures usually result in different topologies in relation to those obtained before the weighting.

As a corollary of these ideas, it is very easy and tempting to generalize and equate levels of homoplasy with confidence in a tree. Thus, these cladists apply these conceptions of reliability in systematics and used it against homoplasy. Before I put these ideas on weighting with our discussion on homoplasy and the evolution, let us have a look at the following quote by Wiley & Lieberman (2011: 199): “Any form of weighting, including equal weighting, assumes certain things about the evolutionary process.” If weighing assumes “certain things” about evolution, thus the weight against homoplasy can be problematic. Let us resume the main points made in the last section about homoplasy, in order to scrutinize if down-weighted homoplasy is a cogent form of weighting: 1) homoplasy is not an error and it exists beyond trees; 2) homoplasy can be due to evolutionary process, that can, in some cases, reflect evidence of the occurrence of adaptation, thus it is a source of important information about the operation of natural selection; 3) homoplasy is not always unreliable and can be informative in certain cases; 4) homoplasy does not constitute an *ad hoc* hypothesis.

Hence, weighing against homoplasy can result in some wrong “things about the evolutionary process”. We could have been down-weighting reliable information (that could support some clades) or some information about the process and history of certain taxa in relation to convergence and analogy (due to adaptation). By doing that, we are, in some way, losing this preciouses information about the history of our characters that could base additional research about its functions and evolution. If we are willing to disregard some of these patterns (traits that can confirm monophyletic groups) and process (homoplasy due to analogy and/or adaptation due to similar environmental and selective pressure), in order to weight them, thus it should be unproblematic to the cladistics that uses this type of reasoning. However, if we are trying to reflect, the best we can, the evolutionary history of the taxa that possess this character and if we want to develop the science of the phylogenetic as a causal one, we should maintain those homoplastic traits and put them to further test in order to know better its interaction (and function) to other characters and its environment to get a fuller understanding of its history.

11.6. Function and Systematics

“[C]ladists have almost universally rejected functional analysis…” (Ridley, 1986: 126) this was written by Ridley in 1986 and, by now, as we entered the 21st century, the situation is in no better shape. Cracraft (1981) made the earlier (and to my knowledge, the only) discussion of this matter. In it, he criticized what was referred as the “functional evolutionary morphologists”. One main line of criticism that Cracraft makes in relation to the detection of “evolutionary homoplasies” prior to the phylogenetic analysis, and then usually remove those homoplasies subsequently from that analysis. The other is in relation to the “knowledge about adaptation”, that was claimed that can be knowable before a phylogenetic tree was inferred. And finally, he affirms that functional analysis cannot be applied to cladistics as characters, because (Cracraft, 1986: 26): “[S]imilarities in function sometimes parallel similarities in structure, but it is the similarity in structure that is the primary empirical basis for a hypothesis of homology.” As argued before, evolutionary explanations should be based on comprehensive, explicit phylogenetic cladograms, because as the Hennigian argumentation goes, the homoplasies should ideally be detected in the face of results of the phylogenetic analysis, and not prior to this analysis.

So far so good for Cracraft and the cladists. However, he made some forward-looking dismissal of function in cladistics, as the following quote showns (Cracraft, 1986: 30): “I have tried to argue that functional biologists have not made a strong case for the need for functional data in phylogenetic analysis. It may be that functional data are important, but this has not yet been demonstrated effectively.” Continuing with the dismissal, he argued that functional morphologists does not study adaptation because they cannot gather the evidence necessary because they are inaccessible. This kind or argumentation is mirrored in the relation of problems of ancestor-descendant relations: cladists claims that it is unknowable while the evolutionary taxonomists claims it is (Hull, 1980). Herein the same strategy was developed: while functions, related to adaptations, are totally unknowable, this is of no avail to cladists, in other words, they do not need (ever) to know whether a trait's function is some indication of adaptation. In the same line argued by Hull (1980), cladists considered that they can know what they it is need to know, i.e., sister-group relations, while everything else about phylogeny is as speculative as the functional morphologists claim. In the same line of argumentation, Cracraft demands that knowledge about (1) heritability, (2) genetic variance and its relationship to intrapopulational phenotypic variability, (3) the relationship between intrapopulational phenotypic variation and (4) variation in fitness and (5) question on atomization of characters shoulb be known to confirm an adaptation. Thus, regarding with the above *desiderata*, he concluded that (Cracraft, 1986: 31): “[F]unctional evolutionary morphology—as well as most other areas of evolutionary biology—is not engaged in the study of adaptation.” He then proceeds to consider a function of adaptation as “untestable”, “intractable” and even as an act of “faith”. But how really problematic are these issues? Are they as totally unknowable as the cladists claim? As showed earlier, within the new “The New Adaptationism” (Rose & Lauder, 1996) or the “Adaptive-historical thinking” (Griffiths, 1996), the comparative method using phylogenetic trees to support hypotheses of homology and homoplasy as a result of the congruence of characters by, for instance, parsimony, we are able to make studies on function that may indicate adaptation. In conclusion, while the first criticism of Cracraft is legitimated by Hennig and the evolutionary process, his other criticism on the inability to make any claims about functions in the evolution of a character is, at best, weak. For the sake of this section, I will bring some themes that will be more scrutinized latter, as in relation to the two components to character evolution: origin and maintenance. Character origin is the result of a phylogenetic tree, in the form of a derived character (homology or homoplasy), while maintenance is the reason, or better, the function (mainly a current function) for the character being select. Thus, when we investigate the evolutionary maintenance of a given trait, we usually prioritize the functional factors, natural selection (or sexual selection, for instance), as the most significant factors in evolutionary research, but not the only one as argued, and we might start with the question: ‘Does this trait have a function?’

Therefore, we are able to know the function of a character. It is knowable after all. Of course, it is not easy to propose a function, and even harder to argue for a trait being an adaptation. But as Hull argued (1980: 135): “[V]iews on the evolutionary process are not easily testable, but no one ever said science was easy. It was not an easy task to devise tests which distinguished between the geocentric and heliocentric theories of the universe, but through several hundred years of trying, scientists were eventually able to present sufficiently conclusive evidence in favor of the heliocentric system.” Of great importance is the *desiderata* of Cracraft (1986), as exposed above, conflate, one more time the epistemological characteristics of a historical science (table 1), in this case, in relation to evolution and phylogenetic trees. When he asks for knowledge about genetic variance and its relationship to intrapopulational phenotypic variability and variation in fitness, he is demanding something that a historical science of macroevolution, in its huge demands of time (in addition to the destruction of its evidence, e.g., DNA), cannot give. Therefore, one more time, Cracraft is **measuring the quality of a historical character by using experimental tools**.

11.7. On the role of Historical Narratives in relation to the testability of adaptation

Functions, because they are the actions of phenotypic components, should be followed by some experimental measurement in the environment for the confirmation about its proper role. This is very important because information about why characters are distributed the way they are on a cladogram is obtained by these interrelations between form and function (Lauder, 1990). After we obtain a well supported phylogenetic tree, with the aid of functional analysis, we can be able to (Lauder, 1990: 321): "[U]nderstand a mechanical system and the causal factors involved in its construction…" Thus, functional information is a major tool for a causal explanation of Why-questions of the presence (maintenance) of characters, which is our way to reach an understanding. A conclusion of this inference is that if we give up functional analysis, a large amount of inferential hypothesis of adaptational will be left aside as well. This happens because adaptation represents one relevant way of the expression of functional explanation in matching form with function (Gans, 1988). As Garson (2019) argued, when we give functions to traits, we a give a causal explanation for why those traits exist. Following Cracraft (1986), cladists stated that functional analysis is unnecessary, and mainly impossible, and should be left alone. But this exclusion has been accomplished mainly by silently overlooking it, or by scattered critical asides, and not by detailed argument (Ridley, 1986). I have shown the problems with this exclusion, and the problematic arguments made by Cracraft (1986) which did not survive scrutiny. Now, we shall see how this dismissal has harmful for the phylogeneticists in relation to evolution and function.

Adaptation was a seriously matter for some authors that worked with cladistics (Coddington, 1988; 1994; Baum & Larson, 1991; Larson & Losos, 1996). I will discuss some of the main conclusion of these authors herein. One of the main flaws that these articles proclaim, is the necessity to, so they argue, make a rigorous **test to adaptation**, in other words, to construct an hypothesis of adaptation (usually only an apomorphy) must be corroborated (not falsified). These authors elaborated protocols for testing hypotheses of adaptation and although their details differ, they share common goals like (Larson & Losos, 1996: 198-200): "(1) the character evolved in the context of a particular selective regime; and (2) that the character is more advantageous than phylogenetic antecedents in that context." The matter of the selective regime is very problematic do say the least. Selective regimes comprise organismal/environmental interactions like abiotic climatic factors, biotic environmental factors or organismal features. The functional analysis can provide information about the interaction between organism (characters) and its environmental (host use, predation). We need to know the actually environment and interaction of a taxa to give a concrete functional explanation. The most information that we can obtain is from the **historical narrative** of the past origin of a trait (more about the structure and methodology of narratives on evolution will be given soon). So as Mayr (1982: 52) argued: "In biology, and particularly in evolutionary biology, explanations ordinarily concern historical narratives.” Smith (2016) described that a historical adaptive explanation is a coherent narrative explanation that requires a chronology and a causal ordering of the events, which are parts of an integrated whole (that can be a trait to be explained in a historical Why-Question).

Another collective problem with their approach is the fully commitment to the popperian philosophy of science. As Baum & Larson (1991: 15) wrote: “[H]ypotheses regarding the causal explanation of character evolution can be tested in a hypothetico-deductive, phylogenetic framework.” Taking testability and falsification as a main *desiderata*, they keenly proceeded by popperian terms, but lacked some characteristics of a narrative explanations, for instance, that “[h]istorical narratives can only rarely (if at all) be tested by experiment.” (Mayr, 1982: 521, see also Smith, 2016 and Olson & Arroyo-Santos, 2015). For the sake of clarity, the classic and well know first definition of what are historical narratives was given by Gould (1989, 283):

“Historical explanations take the form of narrative: E, the phenomenon to be explained, arose because D came before, preceded by C, B, and A. If any of these earlier stages had not occurred, or had transpired in a different way, then E would not exist (or would be present in a substantially altered form, E’, requiring a different explanation).”

And so, as Currie (2013), summarizes it, narrative explanations: “(1) account for some particular *explanandum* in terms of some causal sequence; (2) target a central subject; (3) may or may not appeal explicitly to laws or generalizations; (4) are paradigmatically, but not exclusively, historical.” Later, Currie (2013) contrasted between a ‘simple’ narrative (an event is explained by a general model, and minimal causal factors are referenced) and a ‘complex narrative’ (an event that no appeal to a general model in explanation is made; rather a unique, detailed causal sequence is employed) - snowball earth being the case for the simple case while sauropod gigantism is for the complex one. Evolutionary explanations, thus, are a complex causal narrative explanation. Now it is plain to see that this rigorous popperian test are, indeed very difficult, and at times almost impossible to test. Before going further, we can define testability as some hypotheses that make evidence claims (predictions) about something (directly or indirectly observed) that can be checked by observation (Sober, 1999). However, as is the case of evolutionary biology, and mainly Paleontology, some narratives are causal events more distal in time than others, so it is much more difficult to make a decision about the test evidence available. Sober (1999) raised the point that testability is a changing matter, because as our understanding of the empirical world raises, untestable problems may not remain so. To make a concrete example, Turner (2016) in earlier works had predict that we would not be able to determine the colors of the dinosaurs. However, when scientists (Vinther et al., 2008) were able to study the microstructure of fossil feathers from dinosaurs' melanosomes, they could tell us about its coloration, more precisely, that filaments from the tail of *Sinosauropteryx* has some dark-coloured stripes with reddish-brown tones. This example makes it clear that the epistemology of the historical sciences, as well as the experimental sciences, advance in their methodology and gains access to information previously unable to be obtained. But we still are in great disadvantage in relation to gain access, and test whole other traits and environments. Thus, while most evolutionary scenarios are currently untestable, but testable in principle, we should do two things: not giving up this epistemic bet against historical sciences and be aware of this enhancing of information by new methods (in this case, new fossil finding and/or a new technology); however, we should be equally aware of the tremendous dilatation of time and degradation of information that all life of Earth passed by, so that lots of narratives cannot be tested in this familiarly fashion and we should be satisfied to give all the possible test evidence for some hypotheses (in contrast to a rival one).

Now, with all these new "weapons" we can clearly see that the rigorous "tests" demanded by those cladists, as discussed earlier, mischaracterize the epistemic restrictions of a narrative explanation of adaptation. It is unavoidable. Historical narratives, after we acknowledge their intrinsic limitation, have great explanatory value because earlier events in a historical sequence usually make a causal contribution to later events, so that they can be able to discover causes responsible for subsequent events (Mayr, 1982). There is no single unifying regularity that could be used for explaining particular facts. Another point to note is the relation between narrative explanation and the contingency thesis of Stephen Gould (1989); this became famously defined as: "Two initially identical populations inhabiting identical environments will not have simultaneous, identical mutational histories, and as a result they may diverge evolutionarily." (Beatty, 2006: 342). Alternatively, as Stephen Gould put it, the evolutionary process of all the life on Earth is like a videotape that, if replayed over again, would have a different ending every time (Gould, 1989). Therefore, a historical narrative is contingent in another way: they are necessary in an undeterministic world in which unpredictability events happens all the time (Beatty, 2016).

One final philosophical though is that the nomological-deductive model of scientific explanation of Hempel (1965) will not going to helps us here, one more time. Hempel maintained that history (included the historical narratives) provides us only with “explanations sketches”, that is, as a result of the lawless structure of history (evolutionary biology included) it could not give a complete explanation as it falls to have a logical deduction between the laws and the initial conditions. However, as argued by Hull (1992: 77): “In historical explanations an event is not explained by subsuming it under generalization. Instead, it is explained by integrating it into an organized whole.” In the same line, Richards (1992) affirmed that these explanation sketches are symmetric as a matter of a failure to given complete explanation in the historical sciences as well as the physical sciences because Hempel can give us only a correct deduction but incorrect explanations. Finally, narrative explanation and understanding are a type of causal explanation of past events by making descriptions and hypotheses of historical entities as they persist through time (Hull, 1992). Now that I have cleared these epistemic issues, and before I scrutinize what contributions these cladists made to adaptation hypotheses, I should discuss, briefly, the relation of characters origins in relation to narrative explanations.

11.8. Exadaptation, adaptation and narrative explanation - a case for concern

“The operation of an adaptation is its function.” (Gould & Vrba, 1982: 6)

Gould & Vrba (1982) started their widely cited and discussed article by describing a received view in evolutionary studies, the relation of the historical genesis of a trait in contrast to it's current utility. Later, they considered trait origin, that was unrelated to their current function as very important; so much that they made use of a neology: “We suggest that such characters, evolved for other usages (or for no function at all), and later "coopted" for their current role, be called *exaptations*.” (Gould & Vrba, 1982: 6). They later argued to “reconstruct the historical pathway of its origin”, even recognizing the difficult and even the insolubility of this matter. Gould & Vrba (1982) agree that various adaptations that exist today change their function along time, in other words, are a secondary adaptation of some early adaptations that had different functions; but they also considered traits that had no functions at all (nonaptations), as a phenotypic pool for natural selection to act in new adaptations. In other words, their ancestors did not possessed that adaptation. Exaptation, then, cannot be defined in relation to their current role, because they were constructed originally as nonaptive or as adaptations for different functions. One corollary of the argument made by Gould and Vrba is that a trait is an adaptation only for the purpose for which it was first selected (Sterenly &

Griffths, 1999), if it was first select, for any other function (or no function) they should be named exaptation. Finally, they made the following conclusion: “Adaptations have functions; exaptations have effects” (Gould & Vrba, 1982: 6). This last quote that we are going to critically examine.

Griffiths (1992) argued that Gould & Vrba (1982) made a mischaracterization of the function/effect distinction in relation to the adaptation/exaptation distinction. Every trait arises by random process like chromosomic linkage and mutation, and exists in the population at some low frequency in a population, that can be selected for some function in order to increase its frequency. Even in low frequencies and with some initial function, it presents the effect of a selective explanation of the current maintenance by its function (Griffiths, 1992). If this trait acquires a new function, Gould and Vrba, will called it an effect, because it is an exaptation in their definition. But, if this character had a function (and hence was an adaptation), and was selected because of that, that same trait is an adaptation, in a teleological explanation framework, of the trait existence, independently of its initial function. They are all effects and adaptations, just had different original functions. In the case of originally nonadaptive trait, that became an adaptation, we can call it just an effect, because if it were not select it had no functions, and arose by some non adaptative processes like drift, pleiotropy or morphological (including embryological) constrains. This is the raw material that ‘descent with modification’ can select and chance along time. As Dennett (1995: 248) wrote: “[T]his is how all adaptations get their start, after all, as fortuitous effects that get opportunistically picked up by selective forces in the environment.” The criticism can be amplified in a way that, as it’s the case on the life on Earth, if you go back far enough, you will find that every adaptation has developed out of predecessor structures each of which either had some other use or no use at all, so “every adaptation is one sort of exaptation” Dennett (1995). But after a new function arise in relation to that trait it became a straightforward adaptation, with functions, as the other cases discussed here and by Gould and Vrba. Thus, as Griffiths (1992) argued the asymmetry between a trait that passed by selection or non adaptive reasons, can both be valid selective explanations for these selected effects.

In conclusion, the difference that Gould and Vrba give are, indeed, very important, but for other reasons; I shall argue that the matter here is in relation to the narrative explanation for the history of the trait development. We can say that all functions as adaptations can be called by this name, unrestricted by its origins. But as historical scientists who wants to knows all the history of a trait, we should pursuit a coherent narrative explanation for a historical adaptive explanation. If we want to explain why a change in a trait, and its function, increased fitness its presence in a certain historical contingent context, it is necessary to understand the primitive condition (Smith, 2016). Because the narrative explanations aim at inferring some complex causal components, including the environment and the interactions between the organism that possess that trait, these explanations have limitations. This is all unavoidable, but it should not be an obstacle for the historical scientists (Smith, 2016; Gould & Vrba, 1982; Currie & Sterelny, 2017). So, if a trait was another adaptation or had no function, we call that this same trait **in relation to its origins** was an exaptation or adaptation. If it had no function, it was an exaptation (*sensu* Vrba & Gould, 1982) and if was derived from another adaptation, we should call it an adaptation (primary in this case). I will use the example given by Gould & Vrba (1982) in relation to feather in birds. Herein we can consider that, contrary to the authors that considered the early stages of wing development (as predatory or thermoregulatory functions) as effects (exaptations) for flight, the early stages were adaptation of their own, and were functionally selected. Thus, even if feather for flight are exadaptive in its origin, are adaptive in its actual function. Whenever there is selection pressure for something, there will be selective causal explanations, and, therefore, functions (Griffiths, 1992).

11.9. Cladism and adaptation

Initially, the cladists restrict the study of adaptation for homology, more precisely apomorphic traits, or evolutionary novelties (Coddington, 1988; 1990; Baum & Larson, 1991). This type of analysis became known as the homology approach. Although the understanding of function in relation to homology is appreciated to be important, it only relates partially to adaptation. Instead, homologous and identical function of the trait would be evidence that the origin of function was preserved. On the other hand cladists argues that the function as current utility makes no claims about origin of adaptation. Homoplasy, following the traditional cladistics view, is an *ad hoc* hypothesis and could not be any evidence of relationship, and was dismissed as less relevant, almost as irrelevant, to adaptation. While pointing to some correct cases when convergence is not an act of natural selection - like the blindness of cave faunas (Coddington, 1988) - homoplasy was hardly at status of truly being used as evidence of adaptation (although it was considered as necessary). They focus as mainly in the historical genesis of adaptation or related to the origin of traits, instead of the maintenance of traits. Later, and in contrast with the previously approach, some scientists (Coddington, 1994; Larson &

Losos, 1996) created the convergence approach in order to determine whether multiple independently evolved traits show a phylogenetically correct correlation with a particular selective regime, and this approach, consequently, places greater emphasis on statistical patterns. This is aligned to the definition of "The comparative method" by Harvey & Pagel (1991) that developed these statistical models.

So far, so good. Wenzel & Carpenter (1994) however, raised strongly critics to these statically direct analyses of homoplasy, but stating for the inappropriateness of statistical models for historically unique events. Although Harvey & Pagel (1991: 35) emphasize the need of a phylogenetic tree for getting reliable hypotheses of homology (in contrast to homoplasy) and derived characters (in contrast to primitive ones), they emphasized that: "[P]hylogenies help us to identify independent evolutionary events, and it is independent events that statistical tests rely on." This is important for them because they use species as samples to be used as an independent point for statistical analysis. The relation of optimality criterion is systematics is discussed by some authors, with some arguing for the impossibility of using statistical methods for inferring historical unique events (e.g., Farris, 1983; Brooks & McLennan, 2002)[16].

One of the main tools that cladists argued that could do in relation to the character evolution is in relation to the questions of origin. The power of a phylogenetic tree lies in the ability to disconfirm hypotheses of character evolution (Brooks & McLennan, 2002), more precisely, its origin. For example, a proposal that the evolution of character *x* was influenced by character *y* is falsified if *x* evolved **before** *y*. In contrast, the question of the maintenance of a character is a question about functions, because the functional characterization of the trait says why that trait has caused it to be selected (Griffiths, 1992). Thus, it should be clear be now that acquisition of traits and the acquisition of functions are separate processes, because, one of the reasons being that: "A species may acquire a trait which has no function at all, perhaps due to its genetic linkage with an advantageous trait, and this can acquire functions when the selective environment changes." (Griffiths, 1992: 124). Consequently, the construction of phylogenetic tree represents the only first step, not the ultimate explanation of a character evolution (mainly by the origin issues). In conclusion, "Phylogenies are not the end of the story, merely the end of the beginning." (Brooks & McLennan, 2002: 22), however, they are essential for a comprehensive evolutionary study, because evolution is a temporal process that produces lineages with a past, present, and (indeterminate) future (Brooks & McLennan, 2002). Thus, if

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[16] I will not discuss if this kind of strategy is correct or not herein, but I am inclined in the direction that these authors are indeed correct.

functions of a trait are what that trait is selected for and if biological functions are teleological, as argued herein, mechanisms and narrative explanation must be given as well. Only afterwards on can (possibly) argue for a confirmation that a trait is case of an adaptation. What evidence can we seek in order to confirm if a trait is an adaptation? West-Eberhard (1992) brought some criteria to be regarded as evidence of trait as adaptation if it has : 1) the same form (we can say parallelism) or similar forms (same design) that occurs in similar environments in unrelated species (specially due to convergence); 2) for some characters in a particular context, in which their components can be related mechanically to some particular function in that context (the goodness of “design"); 3) from altering a character experimentally (or eliminated), in order to see how this affects its efficiency in a particular function or environmental condition (a modification of 2) and 4) the efficiency or reproductive success of different forms within a species are compared in the situation(s) where they are hypothesized to function as adaptations. Finally, today it is widely recognized that all these issues are a matter of proportion: some traits are clearly adaptations, and others are clearly not (Griffiths, 1992). The point is what process was imperative for some peculiar trait - for instance which, or a mutually combination, of these four factors acts as evidence of adaption. One lesson that we can reliably state is that “[E]volutionary explanation depends upon systematics” (Lewinton, 2002: 3).

11.10. On mechanisms and interactors: the case in systematics

If, in evolutionary biology, to make a claim about the function of some item is to make a claim about its evolutionary history and if adaptations are connected by functions ascriptions (that help to explain their existence), then adaptation explanations are causal explanations that make satisfactory answer to a teleological question (Brandon, 1990). Brandon (1990) argues that adaptation explanations are thoroughly mechanistic. However, I shall argue that mechanical explanations constitutes a proximate causation of function explanations of adaptation (that we could call as the ultimate causation). In order for something to be a mechanism, it must have a function, then one can argue that **mechanism as a whole serves a function** (Garson, 2019). Thus, in order for a system, or a trait in an organism, to be a mechanism for something, the system must present a function (Lombrozo & Gwynne, 2014). This is what Garson (2019) called the ‘functional sense of mechanism’. This view can help us to reach an adequate understanding of complex patterns of evolution (Autumn et al., 2002); mechanisms, then serve functions, and functions are your cognitive way to understand a trait (in this case, its maintenance). Some examples of mechanisms are the development and underlying genetic information of some character. One of the main achievements of this approach is to understand and test if particular homoplastic trait is a convergence or parallelism.

Gould (2002) discussed extensively the differences in parallelism and convergence, and concluded that parallelism is a 'gray zone' between homology and convergence. This happens because both of these processes share the common feature of presenting perceived similarity in two different taxa. Common ancestry is the main propriety not shared by both; while it is present in parallelism it is absent in convergence. In other words, the difference lies in the causal meaning of their shared developmental machinery or homologous genes; thus, parallel traits due to homologous underlying generators (developmental or genetic), whereas convergent traits are due to non-homologous underlying generators (developmental or genetic) (Gould, 2002; Hall, 2003; Pearce, 2012). As summarized by Gould (2002: 1079): "At the level of an overt phenotypic structure under explicit consideration, parallelism denies homology and asserts independent origin. But, at the level of the generators for the overt feature – the genes regulating its architecture, and the developmental pathways defining its construction – parallelism affirms homology…" With that, we can affirm that only with parallelism there is a true recurrence of phenotypic sameness (and not simply similarity) – traits with discontinuous phylogenetic distribution due to common ancestry (West-Eberhart, 2003). Thus, parallelism is phenotypically and genetically the same, even if phyletically disjunct. Finally, we can consider parallelism as a class of homology (Gould, 2002; Hall, 2003; West-Eberhart, 2003), hence leaving to convergence the cases where the perceived similarity (or design) is not due to developmental and genetic common ancestry.

The case of the digital reduction in salamanders, based on Autumn et al. (2002), will be discussed. Salamanders, alongside frogs, have limb reduction, Caudata has switch from postaxial to preaxial dominance in limb development, in other words, digit one is the last formed in frogs, and amniotes, but digit five is the last formed in salamanders. At first, this was recognized as an adaptation. However, after developmental studies were conducted, it was discovered that digital reduction is a result of developmental truncation, more precisely, as a consequence of the failure of the digit to undergo morphogenesis. Some other researchers discovered that salamanders have much larger genomes than other tetrapods, and this has implications for limb development. One of the consequences of this large genome is the increase in cell volume. This means that some parts of the developing limb are an insufficient number to undergo segmentation. Thus, this is recognized as the reason for this number reduction, so that the adaptive hypothesis was disconfirmed. In conclusion, an understanding of the developmental mechanism of limb reduction of salamanders strongly suggests digital reduction are **evolutionary side effects**. Another conclusion of these studies is that this trait is homoplastic, as it occurs in some groups o frogs as well. And because these frogs passed by a process of miniaturization, the same explanation of development constraints, in relation to cell volume, occurs. But, once again, this is not a homologous trait or any common history. Therefore, the process of miniaturization is the adaptive trait in amphibians, not limb reduction (being just a side effect). History herein passed a signal of descendent: frogs always have the first limb formed while the salamanders are the five one.

This study illustrates the kinds of developmental and histological techniques that can be absorbed and integrated into the repertoires of the sistematists, in order to resolve the study of the origin of traits. As well as molecular biology, this kind of studies can contribute, via technique and interpretation, to several levels of understanding of the structure-function-adaptation relationship. Molecular and developmental approaches are complementary, and useful to expand the scope of organismal biologists in investigating major questions in morphology, for instance, the question about origin and maintenance (Wake, 1992). So if some character is postulated as homologous, and a posterior molecular analysis revealed that, in reality, they are homoplastic because they are formed by very different genetic information, we can disconfirms the first hypothesis (along any kind of evidence if relationship) relatedness. In this way, genetic information is, in various contexts, a mechanical evidence of the pathways of the phenotypic information and can guide our conclusion of confirmation or disconfirmation of homology and homoplasy, including wether the trait is either parallelism or convergence.

Finally, the apparent epistemological causes of morphological/molecular conflict are the lack of a mechanical basis for comparative morphology that can result in disconnection between genotype and phenotype. While function ascriptions are made by the totality of organismal **interactions**, the genetic material is, fundamentally, replicators (Hull, 1988). These replicators (genetic material) aren't units of selection or the causal agents of change of organisms. In contrast, only interactors can be considered as causal agents in the evolutionary process; hence Gould (2002: 620) argues that: [S]ince genes interact with the environment only indirectly through selection upon organisms, and since selection on organisms operates largely upon emergent characters, genes cannot be units of selection when they function in their customary manner as faithful and differential replicators in the process of ordinary natural selection among organisms.” As a corollary of these premises, we one understand the causal nature of selection it is possible ti recognize that **units of selection must be defined as interactors, not as replicators** (Gould, 2002). And finally, Gould (2002: 633) concluded: "Now, if replicators are not causal agents, but are vital for any full account of evolution—then what are they? I suggest that we view gene-level replicators as basic units for keeping the books of evolutionary change—as "atoms" in the tables of recorded results." Genetic replicators act as bookkeeping the information that was select and preserved, just recording the causal results of evolution. Accordingly, the information obtained for functional analysis must not come from replicators, but from interactors; while the genetic material can enhance our mechanical understanding of organisms (for instance, as test evidence of homology and for the whole picture of a pathways of phenotypic traits). Attention must be placed on the analysis of causal interactions among genes, development, and evolution, to get a well confirmed teleological causal explanation of a particular trait.

11.12. Limits to our Knowledge

After all these discussion, restrictions and possibilities, it is worth mentioning our limits in understanding evolution and some of the irretrievable loss of information, in addition to the complex evolutionary patterns that involves many processes (multiple and reciprocal causation), in order to be able to retrieve a well supported hypotheses of trait evolution. There are limits to historical inference; the chains of time have trapped these historical facts with many unresolvable problems - extinction being the obvious one. Thus, it is not possible to "know" that the particular history estimated is the "true" history, although we may be able to say, within a certain degree, that we possess a well supported hypothesis. Accordingly, some phylogenies (mainly the ones based on extinct taxa) will forever be beyond the limits of our understanding and knowledge, because of absence of fossil record (which is true for most taxa) or for technical (or methodological) limitations, as such as those found in molecular biology. When the fossil record gets exhausted, and we reached the limits of populations biology, together with the knowable information that DNA can inform us – this is true because nucleotide substitutions are the most elemental aspect of evolutionary change – (Clegg, 2000), thus quite probably, some broad portion of information will forever remain incomplete. Even if molecular models for inferring DNA substitutions (as such used for constructing a "molecular clock"), that is considered very promising to resolve for various evolutionary problems, e.g., the age of origin of a taxa, are, in a certain level, mathematical truths without empirical content (Rosenberg, 2000); hence, caution is need when applying these methodologies. Genotypic information is bookkeeping information, and not causal "actors" in nature; organism, on the other hand, are the causal "actors" with their structural hierarchy. Thus, we have no shortcut to address evolutionary historical problems; even if we have thousands of millions of sequence data, with very increased statistical power, we still are not secure that we can give complex causal explanations for a lineage; indeed (Lynch, 2000: 226) "[A]ll of these concepts are statistical, not biological, in nature."

As I argued here, the study of adaptation involves analyses at multiple levels of biological organization. Those levels being the causal determination of how homologies functions to be able to give a teleological explanation are rooted in complex networks of gene and ecological interaction. And if biological functions (as adaptations) are not the isolated manifestation of individual genes (Clegg, 2000), then population genetics and "molecular systematics" are necessary (as an experimental science, see table 1) but not sufficient for evolution. The triumph of genetic studies, in relation to the historical nature of evolution, is to acquire an understanding of the "function" of a gene, or, to get its mechanism; yet little can be revealed about the "context-dependent changes" that are necessary to account for evolutionary changes (Clegg, 2000).

Character evolution is, then, knowable and we need to put forward the theoretical and philosophical framework to get the right interpretation of our evidence. I have tried to show that **to reach an understanding we need to give an accurate explanation based on a causal nexus**. For that, teleology, that has empirical and scientific content in Biology, but not in other areas (physics, for examples), is a major tool to reach a cognitive understanding of a trait. Because functional analysis is the operational way to study teleology, they must be backed by valid functional explanations (Griffiths, 1992). Thus, the functional characterization of the trait can give supportive claims of the why the trait was **caused** it to be selected. This is the question regarding trait maintenance. Thus, in order to avoid the pattern of neglecting function analysis by the systematists (Lauder, 1990; also see Diogo, 2004), it is argued by pursuing this functional information can present an understanding of the character (if there are a function) maintenance. Finally, history always matters, and this is manifested by the historical narrative structure of the evolutionary biology.

All these issues are depended of a well-founded hypothesis of trait origin, and a phylogenetic hypothesis can give this information; without it, we should not be able to know if a character is a homology or homoplasy and if it is a derivate or primitive that are essential information for evolutionary explanations. Thus, we have a methodological framework that is temporally directed. First, we have to be able to provide a well-confirmed phylogenetic tree (trait origin) and them we can pursuit the question regarding its function, it can because adaptation, but can be also due to other selective regimes (stochastic or constrains). Of course, there is no methodological magic bullet that solves all the problems of explanations of a trait evolution, but the framework discussed herein is appropriate for a subset of evolution of characters. As Ghiselin (1997) argued, the evolutionary biologists - systematists included - must go beyond what I have been calling confirmation seeking claims (a phylogenetic hypothesis), but must pursue a legitimate causal explanation for any trait in question - explanation seeking claims. Many evolutionary biologists have already implicitly accepted this functional framework on causation in their research practice. This essay, therefore, call for the attention for new aims to be incorporated as major conceptual incorporation of evolutionary theory in systematics. In this essay, as argued, the main challenge is the study of functional teleological causation that is mainly conceptual rather than empirical; thus we already use the heuristical tools to analyze functional causation (as we already have the methodological confirmation-seeking why questions by using an optimality criteria - as parsimony), and we must spread this knowledge about these tools to other fields. Therefore, the reciprocal illumination of different fields of inquiry - like ethology, functional analysis, ecology, molecular and developmental studies - by using and exploiting already-existing analytical tools is advised, rather than creating new rules of research.

Before concluding this essay one concrete example from tachinid flies will be given in order to demonstrate how all these issues discussed until known can be satisfactorily treated.

12. Case study on teleological causal explanations in systematics

12.1. Eggs, functions and tachinids

Before we begin, consider the following argumentation of Dennett (1995: 241):

“Doesn't my assertion [talking about homology within adaptationist assumptions] fly in the face of the claims of those cladists who purport to deduce history from a statistical analysis of shared and unshared "characters"? … Yes, I guess it does, and my review of their arguments… shows me that the difficulties they create for themselves are largely if not entirely due to their trying so hard to find non-adaptationist ways of drawing the sound inferences that are dead obvious to adaptationists. For instance, those cladists who abstain from adaptation talk cannot just help themselves to the obvious fact that haying webbed feet is a pretty good "character" and having dirty feet (when examined) is not. Like the behaviorists who pretended to be able to explain and predict "behavior" defined in the starkly uninterpreted language of geographical trajectory of body parts, instead of using the richly functionalistic language of searching, eating, hiding, chasing, and so forth, the abstemious cladists create majestic edifices of intricate theory, which is amazing, considering they do it with one hand tied behind their backs, but strange, considering that they wouldn't have to do it at all if they didn't insist on tying one hand behind their backs.”

As the full quotation clearly shows, Dennett, as a committed adaptationist, claims that when cladists completely discards adaptation, they entered some problems of explanation; by completely giving up adaptationist explanation (even when we have some good evidence toward its confirmation), is to give up one of the main Darwinian evidence for evolution, one that he used as a confirmation of natural selection: the designed organism that can be explained teleologically by the functions it performs. To abandon this framework is to leave a considerable part of evolutionary biology; sistematists should not fall into the *argumentum ad traditionem* in continuing to disregard adaptational thinking. As Grandcolas wrote (2015: 90): “[the concept of adaptation] is invaluable to evolutionary biology but difficult to study in practice.” In order to show how difficult it is - because it demands phylogenetic, functional, historical, and experimental studies - and at the same time so invaluable to evolutionary biology these adaptational claims are, a case study will be given based on a group of tachinids (Santis & Nihei, submitted).

All tachinids with known life histories are parasitoids of other arthropods, ranging from caterpillars, the most common hosts, to spiders and scorpions (Arnaud, 1978; Guimarães, 1977; Herting, 1960). The extreme host range that tachinids parasitizes and the wide variety of methods by which they coordinate their attack make this family unique among Diptera and parasitoids in general (Stireman et al., 2006). One of these strategies is made through an indirect infection by microtype eggs. These eggs are small (0.4 mm or less), plan-convex, with a polygonal network on dorsal region of the chorion, in addition to a system of tubes and holes; the ventral region is smooth and has grip properties (Gaponov, 2003) that are used to be glued to leaves in order to be accidentally ingested by the hosts, in order to hatch within the intestine (Thompson, 1963). These are known, until now, mainly in Goniini (Exoristinae), and are traditionally regarded as a derived trait, i.e., a putative synapomorphy for this group (Herting, 1957; 1960; Thompson, 1963; Mesnil, 1975; Wood, 1987).

Another instance of these eggs was discovered by the results obtained by Grillo and Alvarez (1984). They were the first to publish on the bionomics of a species of an undescribed species *Cenosoma* Wulp, 1890 (a New World genus belonging to the tribe Oestrophasiini) that parasites adults of *Pachnaeus litus* Germar (Coleoptera, Cruculionidae). In order to determine the form that these beetles end up parasitized, Grillo and Alvarez (1984) performed various experiments; initially, they tested the idea that the strongly modified (piercer) ovipositor of *Cenosoma* could be a signal that it could inject its eggs directly in the body of the beetle. However, the females of *Cenosoma* do not showed any interest in the beetle and this hypothesis was soon was discarded. Afterward, they confirmed that the function of the piercer ovipositor was not to directly pierce and inject the eggs within the beetle. This fact led them to one further experience: they put together just the females of *Cenosoma* and a tender citrus bud (with just a few leaves) in a controlled cage. Soon after, the females were observed conducting the following behavior (Grillo & Alvarez, 1984: 105): "[*C*]*enosoma* females were seen quickly traversing the leaves and finally standing next to the edge, with the head directed towards outside, holding the front legs on the same edge and applied the ovipositor strongly against the blade, about 0.50-0.75 mm from the edge, exercising with the back of the body a rapid vibratory movement to the left and right, for about 5 seconds, then they remained motionless for about 3 seconds; this process was repeated after changing laterally" (my translation). After ending this behavior, the authors examined this particular area of the leaf to found small punctures in the epidermis (Figure 1A and B). When dissecting these leaves, they discovered *Cenosoma* eggs (Figure 1C) within the parenchyma (in groups of 1-3 eggs that were upward directed). And finally, they introduced the beetles (*P. litus*) - that had remained without eating for 24 hours - that ate the area where the parasite's eggs were. One important fact is that *P. litus* always ate puncturing cubiform cuts in the leaves, and this behavior ensures that at least some *Cenosoma* eggs remains intact. Indeed, sometime later, more precisely 22 days later (this is the life cycle of *Cenosoma* from egg to adult), adult females of *Cenosoma* emerged. This was later confirmed by morphology of the ovipositor that was not adapted to deposit eggs or larvae outside or inside the host's body (evidence of adaptation type 4 of West-Eberhard (1992)). The detailed structure, that is related to oviposition behavior, presents the tergite 7 fused with sternite 7, forming a complete structure that probably supports the modified tergites and sternites; sternite is enlarged, bulbous, and bearing four stout spines apically and dorsally with projecting piercer processes posteriorly; the anteroventral surface bearing numerous major setae; sternite 10 is modified into a piercing structure with acutely pointed with apex strongly and curved dorsally (Figure 1D). In the possession of the description of these structures (the pieces of the mechanism), it became clear that (mainly the sternite 8 with the 10) interact with each other to inject its eggs in a precise puncture on the leave. This strategy is a practice that was previously unknown among the Tachinidae (O'Hara, 1985); the modifications of the piercers sternite 8 and 10 function to inject the eggs inside the leaves (evidence of adaptation type 2 of West-Eberhard (1992)). After concluding our hypothesis of the function of this structure a phylogenetic tree and a historical narrative to give a comprehensive understanding of this trait – microtype egg – origin is needed. Some background explanations are given before proceeding to this theme.

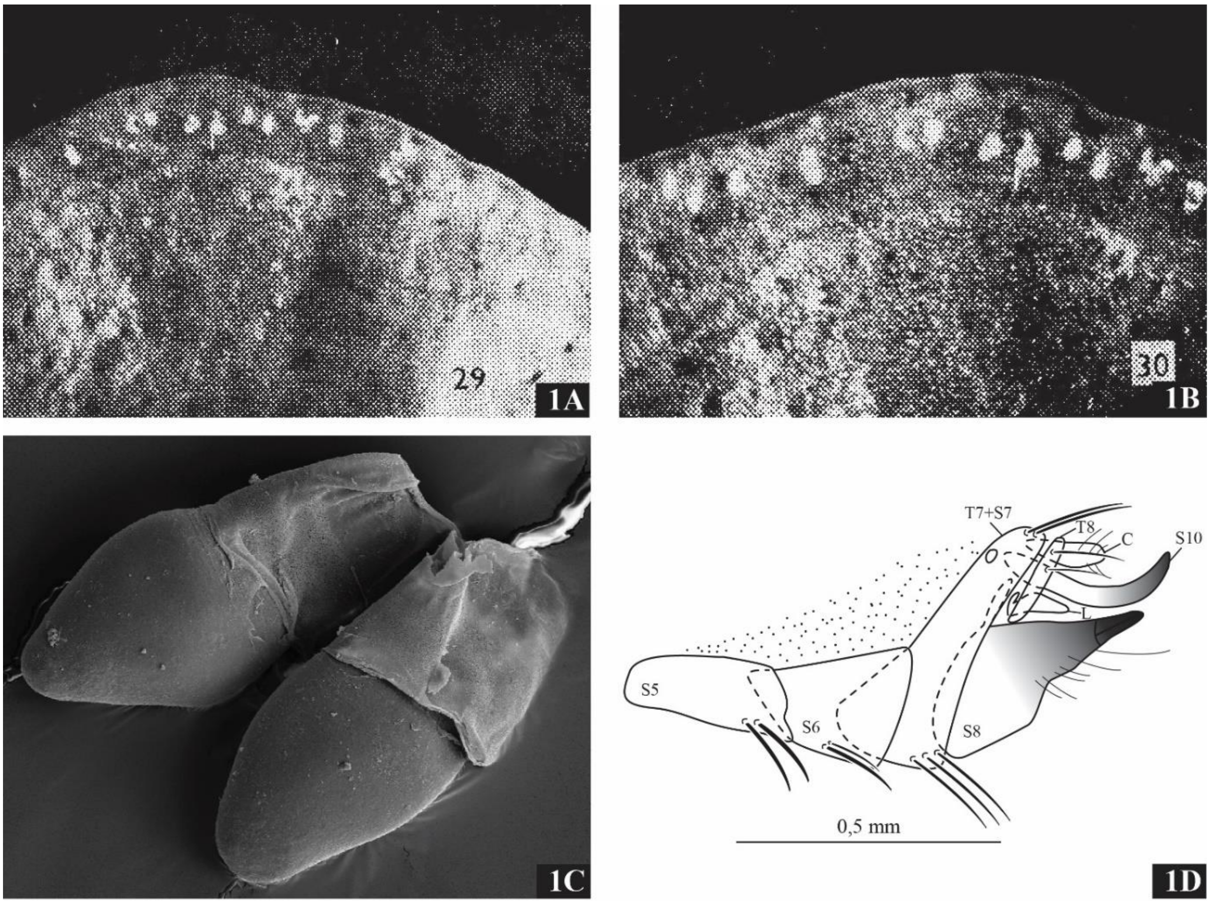

Figure 1. A; B. Punctures in a citrus leaf containing microtype eggs of *Cenosoma* sp (from Grillo & Alvarez, 1984); **C.** Electron microscopy of *Cenosoma thompsoni*, Guimarães; **D.** Female terminalia of *Cenosoma thompsoni*, Guimarães.

One of the subfamilies of Tachinidae is Dexiinae; this is a large and morphologically diverse group, with its larvae almost always parasitizing immatures of Coleoptera or Lepidoptera. In some groups, e.g., Dexiini, the hosts are actively sought by first instar larvae deposited nearby the host by females. This is very probably the cause for the effect of a simple and short female terminalia, with their larvae completing the development in the host and forming a puparium inside of their remains or on the surrounding substrate (Barraclough, 1992). Thus, the infection of immatures is made by the larvae, as the cuticle of these insects is not as strong as the adults (mainly the beetles), the larva is able to infest the host by itself. Their eggs are membranous and are reabsorbed by the females before the larvae are deposited.

Phasiinae as the sister group of Dufouriini (Santis & Nihei, submitted) and this tribe is sister group of Oestrophasiini - a new world tribe that belongs to *Cenosoma* – that possess a related strategy. Some Phasiinae possess macrotype eggs that are characterized by their relatively large size (greater than 0.4 mm) and are plan-convex, i.e., the dorsal surface usually contains a polygonal net, while the ventral surface is smooth and contains adherent substances (to be glued to the body of the host), the first instar larva is not incubated (developing while adhering to the host) (Gaponov, 2003). When the larva is fully developed, produces a chemical substance that punctures the host that enables it to enter in the body of the host, parasitizing it (Dupuis, 1963). This strategy is recognized as an efficient way of overcoming the "bullet proof" cuticle of the very hardened body of the Heteroptera (Hemiptera). The sister group of Oestrophasiini is Dufouriini, that is sister do Frearaini (Santis & Nihei, submitted), and all species of these tribes are characterized as being parasitoids of adult beetles, thus the vast majority of their genera present modified ovipositors in various ways. As a matter of example some of them, like *Rondania* Robineau-Desvoidy (Dufouriini), infect their hosts introducing the larvae from the natural openings (Figure 2A), e.g., mouth (De Fluiter & Blijdorp, 1935). Others, as *Microsoma* (Freraeini), with its piercer ovipositor, infect the host by perforating the epithelium (Figure 2B) and injecting the larva internally (Berry & Parker, 1950). Thus, based on this phylogenetic tree we could postulate that the transformational series of egg within this group followed the path from a membranous egg, plesiomorphic, to a microtype, the apomorphic state. With the support of Phylogenetics, we can reliably state that this was the case (confirmation-seeking why question *sensu* Salmon (1998)).

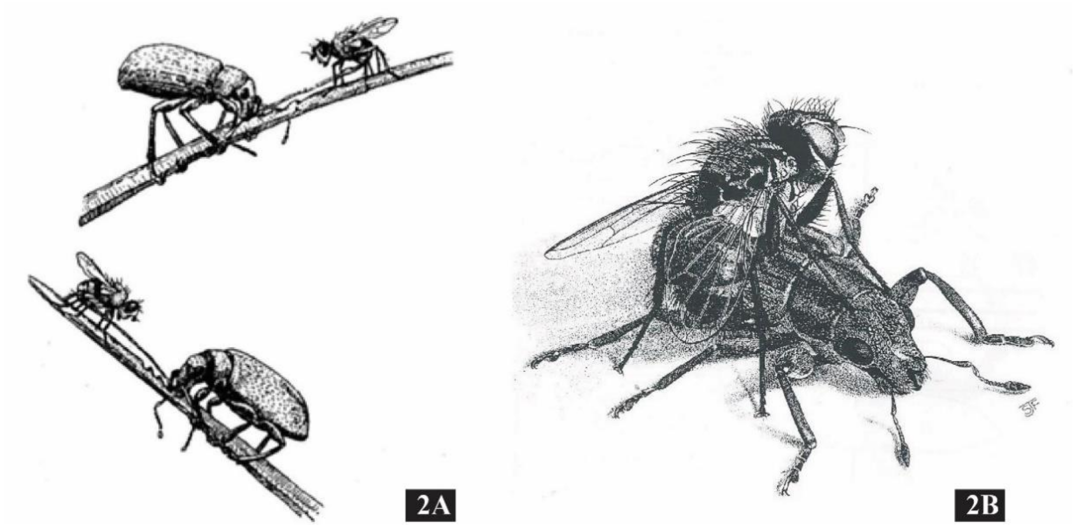

Figure 2. A. The oviposition behavior of *Rondania dimidiata* Meigen, 1824: it transports an egg with her long ovipositor into the mouthparts of *Brachyderes incanus* (Linnaeus, 1758) (De Fluiter & Blijdorp, 1935); **B.** Drawn interpretation of Belshaw (1993) based on Berry & Parker (1950) description of the behaviour of *Microsoma exiguum* Meigen, 1824: this tachinid pierces the thorax of a *Hypera postica* (Gyllenhal, 1813) for injection its larva.

Very importantly is that the presence of a microtype egg is a synapomorphy of Oestrophasiini, and we can regard it as a historical novelty in these lineages (Santis & Nihei, submitted); in past populations these strategies, as found in the extant species of Oestrophasiini, was a different one. As argued, organisms faced with the same problems can result in very different results. So the strategies derived from form-function relations is related to the pool of genetic and phenotypic possibilities available, and may be constrained by the phylogenetic history of the taxon. As Mayr (1983: 328) argued citing Jacob (1977): "Evolution is opportunistic and natural selection makes use of what-ever variation it encounters. As Jacob (1977) has said so rightly: 'Natural selection does not work like an engineer. It works like a tinkerer.'" As a result, the prediction of the ways that these lineages could have the strategy of developing microtype egg to infect the host is very proximate to the impossible.

Therefore, using as weapons all these phylogenetic and function considerations, we can be able to give a coherent historical explanation for the evolutionary appearing of microtype eggs in *Cenosoma*. Based on the phylogeny of Santis & Nihei (submitted), and confirmed in the chapter 2, the ancestors of Oestrophasiini (and *Cenosoma*) possessed the membranous egg and the selective pressure was directed to the infecting of adult beetles. One successful strategy conducted by these taxa was piercing a citrus leaf in order to inject its eggs that were going to be swallowed by some adult beetles. As this behaivour is still performed (trait evolution pertaining to maintenance questions showed by empirical studies) and have determined function (a very effective weapon to overcome the "hard" defenses of beetles). Of course, we have some open questions: why Dufouriinini, as some Phasiinae, began to switch its hosts to adult insects? Why *Cenosoma* acquired its behavior of injecting the eggs within citric leaves, instead of injecting its eggs, as *Rondania*, in the mouth of the beetle, or as *Microsoma*, injecting its larva directly on the host[17]?

As a conclusion, we can say that **the presence of microtype eggs in *Cenosoma* and injecting its eggs inside the citrus leaves are adaptations**, in order words, it is adaptative because we could give a teleological causal explanation (along with its mechanism), in addition to describe its functions. One further evidence that this is an adaptive trait can be done by using the convergence approach: by comparing the form-function relation in relation to Goniini that, as shown, possess microtype eggs as well. Thompson (1963) argued Goniini with its microtype eggs are very characteristic, being a unique adaptation to larval parasitism in Tachinidae. The author reported some other typical characteristics associated with this type of egg: high egg production (3000 to 5000 eggs) because of the high mortality rate; ovary with many ovarioles, about 80, each containing about 10 to 12 eggs; large tracheal network to provide oxygen needed to support all larvae; desiccation protection (for eggs placed on the leaf surface); the larva should always emerge exclusively in the host intestines. In a previous paper, Thompson (1924) studied the first instar larvae of this egg type and reported their main characteristics: they are 0.45 mm long; antenna and posterior spiracle extremely small; a unique arrangement of spines that generally form short lines on the ventral surface and complete rings in anterior and posterior segments; transparent and colorless cuticle, having rows of hooks at the ends of the first two thoracic segments; segment I, extremely well developed and pigmented; base and narrow and elongated ; full bands of thoracic hooks.

From these different pieces of evidence provided for the egg by Gaponov (2003) and Salked (1980), the internal morphology of female and larva by Thompson (1963; 1924), the eggs of the *Cenosoma* can be compared to see if they also have these characteristics. Thus, the eggs species of Oestrophasiini have: a very small size (less than 0.4 mm in length); are

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[17] We may not have this answer now, actually we could not never have an answer because, as I argued, much historical information is lost (and could be completely lost). But this questions are legit and we must pursue it to have an fuller understanding of trait evolution.

produced in high quantity (between 2000 and 3000); ovary with more than 100 ovarioles (Grillo & Alvarez, 1984); wide network of tracheas; larvae with extremely small antenna and posterior spiracle, clear and colorless cuticle, having rows of hooks at the ends of the segments in the first two thoracic segments; segment I, extremely well developed and pigmented, with the rest of the body without spines. Therefore, it is clear that we are dealing with a remarkable case of morphological convergence. The amazing resemblance of the egg, internal morphology, and the larva, are compelling evidence (evidence of adaptation type 1 of West-Eberhard (1992)) that this is indeed an **adaptive convergence**.

To end this case study, I will quote the following observation made by Williams (1994: 34): "Features may remain associated in phylogeny for purely historical, rather than functional reasons…" He then argues that some traits are present in a taxon by its "phylogenetic legacy", that do not have adaptive functions anymore, so make no "sense", and are to be regarded as to as effects of "past adaptations". I shall discuss one instance of this phenomenon herein. *Cenosoma* eggs (as well as *Oestrophasia* and *Euoestrophasia*) are smothh, they do not have a dividing line (seam) delimiting the dorsal surface of the ventral, which is characteristic of Goniini with microtype eggs. This is due to the question of origin of these eggs: in Oestrophasiini, based on the cladistic analysis of Santis & Nihei (submitted), are derived from ancestors with membranous eggs, which do not have this division, whereas Goniini eggs are derived from ancestors (Exoristini) that had macrotype eggs with this line (Gaponov, 2003). Therefore, the "phylogenetic legacy" of Goniini is the presence of this seam.

13. A Philosophical Epilogue or How to Make Our Ideas Clear

I have been in a long argument to persuade systematists that using functional analysis, the ontological framework to have a teleological causal explanation, contitutes a cognitive understanding of the our why-question for a trait evolution. Some may say this is a philosophical position, and by the reading the same essay, other can say that it is not - it would be just a scientific result based on critically evaluating the state of the art in systematics. My response would be that it is both. The discourse of philosophers of science is just as critical as that of scientists. We can say that science and philosophy of science are more than closely connected. They mutually interpenetrate each other (Hull, 1988), and can fruitfully interact to crictically evaluate the scientific enterprise in various leves (Pigliucci, 2008); as Dennett (1995: 21) worte: "There is no such thing as philosophy-free science; there is only science whose philosophical baggage is taken on board without examination". If philosophy, or theoretical biology, is to make our ideas any clearer, what exactly then am I proposing? A new switch of rules of confirmation? A new methodology? Or a new aim in systematics? Before I can answer that, I will discuss how an American philosopher of science, that studied the levels of a scientific inquiry, cleared these issues.

This philosopher is Larry Laudan (born 1941), author of Science and Values (1984). In this book, he developed what became known as the reticulated model of scientific rationality. I will describe, very briefly, how his model works and how it is structured. He argues against philosophers like Carnap, Hempel, and Popper, that according to Laudan uses the hierarchical model of justification. This model describes that disagreements in science happen at the one level of the hierarchy, namely in the methodological rules. Sometimes, however, scientists disagree over witch methodological rules to use. When this happens, consensus is forged by going up one more rung in the hierarchical ladder to the level of shared aims or goals. According this model, aims are viewed as the final court of appeal. If aims change, the change is not, then, a rational one. Laudan's model, **a triad consisting of theory (factual-theoretical level), methodology (a set of rules), and axiology (i.e., the level of the ends, aims and goals of a particular field of science)**, replaces this hierarchical model. On this model, each of these elements influence one another: justification flows both upward and downward in the hierarchy. This model would provide a better picture of what actually happens in science by capturing the complex process of justification in these three levels of scientific change. In the reticulated model, no one level is more privileged than another. Thus, aims are no longer construed as inflexible; theories and methods inform aims, just as aims inform theories and methods. As Laudan (1984: 62) argues: "The reticulational approach shows that we can use our knowledge of the available methods of inquiry as a tool for assessing the viability of proposed cognitive aims."

This model had some critics but can be of great heuristical value to describe in what level my proposition could be related. Am I intending to make a new theory of function or of systematics? The answer is not at all; I have been using and articulating theories, factual research groups and traditions, to be incorporated in systematics (and vice versa). But then, Am I proposing a new set of methodological rules? The answer is, again, no; I have accepted, for example, the optimality methods of systematics, of population genetics and the experimental epistemology to the mechanical functioning of traits and systems. Finally, Am I to be interested in making new goals, objectives to systematics? Now, the answer is yes. My essay is about changing the aims in systematics. It is just not enough to state that a character is a homology or synapomorphy; if it is a homoplasy or convergence. We should aim at pursuing, with the inexorable historical and methodological difficulties and limitations, a holistic explanation to answer our why-question. However, if we accept that understanding is a cognitive goal; and, in order to make a comprehensive explanation of a trait, is to give a teleological functional explanation, this *desideratum* should be a fruitfull framework. Therefore, this aim should inform theories and methods in evolutionary biology.

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Capítulo 2

Phylogenetic hypothesis for the subfamily Dexiinae (Diptera: Tachindae)

Abstract

A phylogenetic hypothesis is proposed for higher-level relationships within Dexiinae (Tachinidae), based on a 152 species from 107 genera representing all 12 current recognized tribes. Our analysis included a total of 212, parsimony informative, morphological characters from the egg (2), first instar larva (30), adult external morphology (97, excl. terminalia), female terminalia (19), male terminalia (59) and spermatheca (2). One of the outstanding results of our study is the confirmation of the proposition of some authors that Dufouriini, do not belong to Dexiinae nor Phasiinae. According to the results obtained herein, the following tribes are removed from Dexiinae: Oestrophasiini, Freraeini and Dufouriini, constituting now their own subfamily, Dufouriinae (status revalidated), sister group of Phasiinae. The other main result, is that the Voriini *sensu lato* is polyphyletic, and in order to propose this tribe as a monophyletic, we have revalidated Campylochetini **tribe rev**., Eriotrichini **tribe rev.,** Phyllomyini **tribe rev**., Thelairini **tribe rev.** Spathidexiini **tribe rev.** and Wagneriini **tribe rev**.; the Voriini *sensu stricto*, by our newly classification, is monophyletic. Three taxa with historically doubtful classification, Eutherini, Epigrimyiini and Imitomyini, become strongly confirmed as Dexiinae for the two former tribes and Phasiinae for the last. On other hand, Doleschaliini and Rutiliini are nested within Dexiini and are put in synonymy with Dexiini. The tribes Dexillini, Theresiini, Trichodurini, Trixodini, Prosenini and Zeliini, are confirmed as invalid and are considered as synonymous to Dexiini. The genera *Microchaetina*, *Pseudodexia* and *Polygastropteryx* are removed from Dexiinae; the former two genera *incertae sedis* Tachininae and the later *incertae sedis* in Tachinidae. Finally, *Opsophagus* Aldrich is revalidated and taken from the synonymy from *Cyrtophleba* Rondani.

Key words: Dexiiinae; immatures; morphology; systematics; Tachinidae.

Resumo

Uma hipótese filogenética é proposta para relacionamentos de alto nível dentro de Dexiinae (Tachinidae), com base em 152 espécies de 107 gêneros representando todas as 12 tribos atualmente reconhecidas. Nossa análise incluiu um total de 212, parcimôniamente informativos caracteres morfológicos do ovo (2), larva de primeiro ínstar (30), morfologia externa adulta (97, excl. Terminália), terminália feminina (19), terminália masculina (59) e espermateca (2). Um dos resultados mais marcantes de nosso estudo é a confirmação da proposição de alguns autores de que Dufouriini, não pertence a Dexiinae nem a Phasiinae. De acordo com os resultados aqui obtidos, as seguintes tribos são retiradas de Dexiinae:

Oestrophasiini, Freraeini e Dufouriini, constituindo agora sua própria subfamília, Dufouriinae (status revalidado) sendo um grupo irmão de Phasiinae. O outro resultado importante, é que Voriini *sensu lato* é polifilético, e para propor esta tribo como monofilética, revalidamos as tribos Campylochetini **tribe rev**., Eriotrichini **tribe rev.,** Phyllomyini **tribe rev**., Thelairini **tribe rev.** Spathidexiini **tribe rev.** and Wagneriini **tribe rev**.; o Voriini *sensu stricto,* como resultado da nossa nova classificação, é monofilético. Eutherini, Epigrimyiini e Imitomyini que tem classificação historicamente duvidosa, tornam-se fortemente confirmados como Dexiinae para as duas tribos anteriores e Phasiinae para a última. Por outro lado, Doleschaliini e Rutiliini foram recuperados em Dexiini e são, seguindo essa hipótese filogenética, colocados em sinonímia com Dexiini. As tribos Dexillini, Theresiini, Trichodurini, Trixodini, Prosenini e Zeliini, são confirmadas como inválidas e são consideradas sinônimos de Dexiini. Os gêneros *Microchaetina*, *Pseudodexia* e *Polygastroptery* são removidos de Dexiinae; os dois primeiros gêneros *incertae sedis* em Tachininae e o último *incertae sedis* em Tachinidae. Por fim, *Opsophagus* Aldrich é revalidado e retirado da sinonímia de *Cyrtophleba* Rondani.

Palavras-chave: Dexiiinae; imaturos; morfologia; sistemática; Tachinidae.

1. Introduction

Tachinidae is one of the largest Diptera families, with 8592 valid species (O'Hara *et al*., 2020). Tachinid flies are inserted in Oestroidea, which belongs to the Calyptratae, one of the largest and most diverse groups of Diptera (Kutty *et al*., 2019). In addition to Tachinidae, Calliphoridae, Mystacinobiidae, Sarcophagidae, Rhinophoridae and Oestridae (Yeates & Wiegmann, 1999; Stireman *et al*., 2006), this last one a robust monophyletic group (Pape, 1992; Marinho *et al*., 2012; Kutty *et al*., 2019), are included in Oestroidea.

The monophyly of Tachinidae is traditionally established with at least two putative synapomorphies: a well-developed subscutellum in the adult and the labrum extended forward and widely fused with the rest of the cephaloskeleton in the first larval instar (Wood, 1987). Cerretti *et al*. (2014) performed the first phylogeny for the family using cladistic methodology and recovered six additional synapomorphies besides the confirmation of these two synapomorphies. Four subfamilies are recognized in Tachinidae: Exoristinae, Phasiinae, Tachininae and Dexiinae (Herting & Dely-Draskovits, 1993; O'Hara & Wood, 2004; O'Hara & Cerretti, 2016; O'Hara *et al*., 2020), even if there was formerly a proposal for two other subfamilies, Voriinae (Mesnil, 1966; Richter, 1987) and Dufouriinae (Verbeke, 1962; Crosskey, 1976; 1980).

The subfamily Dexiinae is a large and morphologically diverse group, with its larvae almost always parasitizing Coleoptera or Lepidoptera larvae. The subfamily is distributed worldwide (Cantrel & Sabrosky 1989, Crosskey 1976, Guimarães 1971, Herting & Dely-Daskovits 1994, O'Hara & Wood 2004, O'Hara & Cerretti, 2016; O'Hara *et al.*, 2020) and contains 1495 species in about 287 genera (O'Hara *et al.*, 2020). This number is due to the world check list recorded by O'Hara *et al.*, (2020) and is due to some generic systematic placements, alongside unpublished synonymous taxa, which was made by the authors. Our position is to incorporate these modifications, but we note that this work is a checklist and does not give a reason (phylogenetic or not) or evidence for the tribal placement of genera. As the checklist of O'Hara *et al.* (2020) is made on a world basis, the views of these authors are considered as compilations of tachinid classification after the published phylogenies (Cerretti *et al.*, 2016; Blaschke *et al.*, 2018 and Stireman *et al.*, 2018), therefore we are going to use a comparative basis for our analysis herein. In it, Dexiinae is composed of 12 tribes: Dexiini, Doleschallini, Dufouriini, Epigrimyiini, Eutherini, Freraeini, Imitomyiini, Rutiliini, Sophiini Telothyriini, Uramyini and Voriini. However, Imitomyiini is an ambiguous and problematic taxon, being considered as Phasiinae in Cerretti *et al.* (2014) and Blaschke *et al.* (2018), nevertheless it was recovered in Dexiinae by Stireman *et al.* (2018). The last great difference is the suppressing of the tribes Thelairini, Camplylochetini and Wagneriini (*sensu* Crosskey, 1976) for a single one, Voriini. Finally, the subtribes Rhamphinina, Stominina, Phyllomyina and Eriothrixina of Mesnil (1966) the the Zeliini and Trichodurini of Townsend (1934–1942) were all condensed within a larger Voriini and Dexiini respectively.

Tachinids are all endoparasitoid and their larvae develops predominantly in insects like Lepidoptera, Coleoptera, Heteroptera, and Hymenoptera. They have evolved many adaptations related to host location, fecundity, and larval type, that lead to a diversity of oviposition strategies: eggs directly laid on or in the host; an active first-instar larvae that seek out the host to infect it (Stireman et al., 2006); microtype eggs laid on the host food-plant which are then accidentally ingested by the host while it is feeding, like in the Neotropical Oestrophasiini - newly discovered by Santis & Nihei (submitted). These strategies have been considered an important factor in the evolution and diversification of tachinids because they allow inaccessible hosts to be parasitized and enhance their evolutionary plasticity of host range (Cerretti et al., 2014). Hence, tachinids are an important group economically, having successful cases globally as control agents (Grenier, 1988), comparable with the families of parasitoid Hymenoptera (Eggleton & Belshaw, 1993). Comparative study of tachinids, particularly the evolution and adaptations of morphological strategies of their host use, will help us to better understand their ecological roles and aid in predicting host associations for taxa in which hosts are unknown, and that can be potentially used as pest control. Thus only with a reliable taxonomy and phylogeny one can make more accurate prediction about which species to target for investigation. In Dexiinae, in countries like Brazil and Colombia, natural biological control is used by utilizing some species of *Billaea* (Dexiini) as a control of *Rhynchophorus palmarum* (L.) palm weevil, which is one of the most important coconut and palm oil pests in Tropical America, which causes relevant economic losses (Moura *et al*., 1993; Moura *et al*., 2006). Although tachinids are generally beneficial, they can also cause economic damage. This is especially true for certain silkworm parasitoids that are used in commercial silk production (Kumar *et al*., 1993). As briefly shown, despite the ongoing interest in species-level economic importance of Dexiinae, current studies, mainly the phylogenetic ones that uses Neotropical taxa, are mainly limited by taxonomic and systematic impediments, including unknown phylogenetic hypotheses for most tribes, and poorly known generic limits.

1.1. History of phylogenetic analysis of Dexiinae: in search of its sister group

For a long time, the only intuitive hypothesis for the sister group of Dexiinae was from Verbeke (1962), as Dexiinae and Voriinae being close related to Phasiinae, and Herting (1966, 1983), that considered the relationship Tachininae + Dexiinae based on the structure of the membranous egg (both with ovolarviparous larva). Later, in one more intuitive approach, Dexiinae were proposed as the sister group to Phasiinae by Shima (1989) based on the oviposition behavior. However, he only gave one putative synapomorphy to support his ideas; ovoviviparity in Dexiinae and oviparity for Phasiinae. The straighforward conclusion is that early authors as Herting (1966), Mesnil (1966), Verbeke (1962) - and we can include the diagrams of Shima (1989) - are not "phylogenetic trees", but are, actually, “only diagrams of typological relations” (*sensu* Hennig, 1973). Later authors, includind the detailed study of the puparia and larval cephalic skeletons of Tachinidae published by Ziegler (1998), study of male postabdomen of Tachinidae by Tschorsnig (1985), could not find any putative synapomorphy that could support the monophyly of the Tachininae + Dexiinae. Although both authors cited Hennig (1966) and his methodology, neither are grounded in modern phylogenetic theory, i.e., they did not used a Hennigian character polarization based on out group criteria (constructed in a matrix of characters), or a sister-group relationship based on apomorphic character states and did not searched for the shortest trees using the cladistic version of the principle of parsimony. Only in the early 21st Century that phylogenetic studies were published, but this time based on molecular data. The Exoristinae were subject of Stireman’s (2002) molecular study of genes 28S rRNA and EF-1α and by Tachi and Shima (2010), using white, 18S, 28S and 16S rDNA.

The first morphological phylogeny of Tachinidae had to wait over 12 years, in relation to the molecular study of Stireman (2002), to see the light in the publication of Cerretti *et al*. (2014)[18]. They conducted a comprehensive morphological analysis of the family dealing most with Paleartic taxa from the four subfamilies. One of their results was that Dexiinae, with Voriini paraphyletic in relation to a monophyletic Dexiini, was recovered as paraphyletic in relation to Phasiinae. The traditional putative synapomorphy of Dexiinae (basiphallus with a membranous connection with the distiphallus) was not confirmed as synapomorphic by Cerretti *et al*. (2014), this character state was interpreted as having undergone a reversal, being secondarily lost in most Phasiinae. Therefore, in the first test of this trait, i.e., a congruence test with all other traits through a parsimony analysis, confirmed the doubts expressed by Tschorsnig (1985) that pointed that other traits like the ones from its biology and the external features of the adults were different and not as stable as this trait in the male terminalia. In contrast to previously thought, this character state was a synapomorphy — the dexiine-type phallus — in supporting the clade Dexiinae + Phasiinae. This paraphyly of Dexiinae occurred because of a paraphyletic Dufouriini, suggested as more closely related to the Phasiinae. Treated traditionally as Phasiinae (Guimarães, 1971; Crosskey, 1976; Herting, 1966; 1984) because of the presence of macrotype eggs, the Eutherini, on the other hand, was hypothesized as within Dexiinae by the structure of the male terminalia (Tschorsnig, 1985), i.e., pregonites, postgonites and distiphallus. However, in contrast to all these hypotheses, Eutheriini was recovered within Exoristinae by Cerretti *et al*. (2014).

Later, Blaschke et al. (2018) published a molecular phylogenetic analysis for Phasiinae. For this analysis, they used four genes: carbamoyl-phosphate synthetase 2/rudimentary (CAD), lethal giant larvae (LGL), methyl-accepting chemoreceptor (MAC), and molybdenum cofactor sulfurase (MCS) and used both Maximum-likelihood and Bayesian analysis. In this work, the authors recovered Dexiinae as sister to Phasiinae, while making some Ancestral State Reconstruction for seven ‘evolutionarily significant’ traits, two related to Dexiinae: the connection of basiphallus and distiphallus, if it is sclerotized or membranous and hinged or membranous and not hinged; the other is in relation to the presence or absence of platiform

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[18] Cerretti *et al*. (2014) was published almost sixty years after Hennig (1966), thus this family is a very late Dipteran group to have been included in a modern phylogenetic tree based on morphology.

pregonites. In their analysis, they recovered Dexiinae as monophyletic with Imitomyiini placed in Phasiinae.

The most recent phylogenetic analysis for Tachinidae is based on molecular (Stireman *et al*., 2018). They used four nuclear loci and sampled 504 taxa from around the world using Maximum Likelihood and Bayesian analysis; for Dexiinae they sampled Voriini, Dexiini, Dufouriini, Freraeini, Telothyriini, Campylochetini, Uramyini, Thelairini, Etheriini, Epigrimyiini, Rutiliini, Doleschallini and Sophiini. However, while some tribes were satisfiable sampled, for instance Voriini with 12 genera, and Dexiini with 21 genera, some tribes were under sampled, like Telothyriini with just one undetermined species of *Telothyria* Wulp, 1890, and Sophiini with *Cordyligaster septentrionalis* Townsend, 1909. This study, one more time, recovered Dexiinae as sister group of Phasiinae, but contrary to Blaschke *et al*. (2018) with Imitomyini within Dexiinae. As more tribes and genera were sample in relation to last works, some tribes showed to be polyphyletic, even so that the authors claimed that Dexiinae's tribal classification is likely to need a major revision, as Voriini and Dexiini were the polyphyletic groups - the former appearing in five distinct places in Dexiinae clade, and have one of its genera as belonging to Tachininae (*Microchaetina* Wulp, 1891), and the second in three places in the Dexiinae clade, as well as a genus belonging to Tachininae (*Eulasiona* Townsend, 1892). In contradiction to Cerretti *et al*. (2014), Eutheriini was recovered within Dexiinae by Stireman *et al*. (2018).

1.2. Objectives

The general objective of this thesis 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, to determine wheter Phasiinae are the sister group of Dexiinae, and wheter Dexiinae are monophyletic.

The more specific objectives are to delimit the following ambiguous tribes, in order to propose a well supported systematic placement in subfamily and tribal level:

1) Are the Eutherini, Epigrimyiini a clade of Dexiinae or Phasiini?

2) Are the tribes Campylochetini, Eriotrichini, Phyllomyini, Thelairini and Wagneriini (Mesnil, 1974; Crosskey, 1976) non-monophyletic, and best placed within a large Voriini?

3) Are the tribes Prosenini, Theresiini, Trichodurini, Trixodini and Zeliini of Townsend (1934–1942) non-monophyletic, and best placed within Dexiini?

4) Are the subtribes Rhamphinina, Stominina and Eriothrixina of Mesnil (1966) non-monophyletic, and best placed ranked as tribes or as subtribes in Voriini?

5) And finally, to perform a more detailed analysis on the Voriini and Dexiini that were recovered as polyphyletic in Stireman *et al*. (2018). The present study comprises a worldwide sample (with emphasis on Neotropical region) of Dexiinae species (table 1) and can therefore test the homologous characters that have been historically used to designated Dexiinae, e.g., Verbeke (1963) and Tschorsnig (1985), for groups geographically restricted and poorly known tribal taxa.

2. Material and methods

Studied material

The examined specimens belong to the following institutions: ARC - *Arthropod Research Collection*, Michigan State University, Michigan, USA; CAS - California Academy of Sciences, San Francisco, USA; CEIOC - Coleção Entomológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; MNCR - Museo Nacional de Costa Rica, San José, Costa Rica (formerly Instituto Nacional de Biodiversidad - INBIO); MNRJ - Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; NHM-UK - *Natural History Museum*, London, England; DZUP - *Coleção de Entomologia Pe. Jesus Santiago Moure*, Curitiba, Brazil; MZSP - *Museu de Zoologia da Universidade de São Paulo*, São Paulo, Brazil; INPA - Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; UEFS -Universidade Federal de Feira de Santana, Feira de Santana, Brazil; ZMHB - *Berlin Museum für Naturkunde der Humboldt-Universität*, Berlin, Germany.

Specimens collected in the Brazilian states of Mato Grosso, Mato Grosso do Sul and Rondônia from the SISBIOTA-Diptera Project (CNPq-FAPESP), coordinator Carlos Lamas, vice-coordinator Silvio Nihei, were also examined. This material is deposited at MZSP.

Morphological study and terminology

To study the male postabdomen, the specimens were carefully dissected from the fifth segment to avoid damaging the sixth tergite and to maintain the integrity of the abdomen as much as possible. To study the female abdomen and obtain the spermathecae, first instar larvae and/or eggs, the abdomen was dissected from the fourth segment and rarely in the third. The male terminalia were bleached in 10% potassium hydroxide solution (KOH) for four minutes in boiling water, neutralized with 5% acetic acid solution and washed with water. The female terminalia, larvae and eggs were subjected to a similar procedure, except they were heated for 10 minutes in 10% KOH solution. At the end of the procedure, the material was preserved in glycerin, packed in microplastic vials and pinned to the respective specimen.

To study adult morphology, dried and pinned specimens were examined under a Leica EZ4 stereomicroscope. A Leica MC170 HD digital camera attached to a Leica MZ16 stereomicroscope was used to analyze postabdomen, first instar larvae and eggs. The terminology of adult and spermathecae morphology followed Cumming & Wood (2017). The terminology of first instar larva followed the nomenclature proposed by Thompson (1963), with some modifications discussed by Cantrell (1988). The term "cephaloskeleton" from Courtney *et al*. (2000) was used.

Selection of taxa

To select the terminals of the internal group, three premises were considered: (1) the availability of specimens for morphological study; (2) availability of immature stage material (e.g., first instar larvae), and (3) differences in geographic distribution and morphology. Our goal was to collect species of representative genera of every tribe (valid and invalid) within Dexiinae. With the inclusion of 105 genera, all 12 tribes currently valid in Dexiinae, in addition to another 15 tribes (and subtribes) that are currently treated as invalid, this goal was achieved. In total, 150 species of Dexiinae were included as the ingroup; while the outgroup constituted of 10 species, within those taxa, all other subfamilies of Tachinidae were sampled: Exoristinae (*Winthemia* and *Lespesia*); Tachininae (*Archytas*, *Cholomyia*, *Eutrixa*, *Irengia*, *Palpostoma* and *Uruleskia*) and Phasiinae (*Eutrichopoda*, *Leucostoma*, *Imitomyia* and *Phasia*). As this analysis is about the phylogeny of a subfamily of Tachinidae, *Calliphora vomitoria* (L., 1758) was selected as the root for the analyses as calliphorids (mainly the subfamily Polleniinae) has been contantly recovered as the sister group of Tachinidae (Kutty et al. 2019; Bunaventura et al., 2020). Tables 1 and 2 show the terminals included in the cladistic analysis with geographical distribution and number of species in each genus.

Cladistic analysis and character coding

The study of phylogenetic relationships was based on morphological characters of adults (including female and male genitalia and spermathecae), first instar larva and egg and puparium, which was based on parsimony as the optimality criterion. When found appropriate, some characters were constructed according to the proposal of Sereno (2007), with preference for the contingent coding (Forey & Kitching, 2000). For taxa lacking a particular structure, transformational character states are encoded with a " - " for the inapplicable condition and “?” for unobserved data. The data and putative synapomorphies of the male terminalia presented by Tschorsnig (1985) were reanalyzed and included within a cladistic framework. Characters from literature, e.g., Cerretti *et al*. (2014), have been properly indicated in the character list.

The polarization was conducted using the method of outgroup comparison (Nixon & Carpenter, 1993). The matrix of characters was built with *Mesquite 3.6* software (Madison & Madison, 2018). For the parsimony analysis using equal and implied weighing, the *TNT 1.1* software (Goloboff *et al*., 2008) and the strategies of the New Search Technology (Ratchet, Drift, Tree Fusion and Sectorial Searches) were used. The analysis was performed according to the following parameters: random seed = 1; number of replicates = 10,000; number of trees saved per replication = 10. The software *Winclada 1.00.08* (Nixon, 2002) was used to display the trees with the transformation series of each characters, in addition to their optimization. For the MP tree under equal weights, we provide the total length (L), the consistency index (CI) (Kluge & Farris, 1969) and the retention index (RI) (Farris, 1989), calculated from all characters.

Parsimony criterion of Fitch (1971), which treats the characters as unordered (or non-additive), was used in this study. Autapomorphic characters were maintained in the analysis. Implied weighing (Goloboff, 1993) was used to observe how the characters behave as different weighing schemes, based on the fit measure of each character and its overall fit of the topology. However, as argued by Goloboff (1993), there is no known well-justified criteria to choose some particular value of K, and it is, probably, matrix dependent; thereby, the k-values of 1, 2, 3, 5 and 10 were tested. Branch support was checked using Bremer support (1994), with the “Bremer.run” script provided in the TNT Software Wiki (http://phylo.wdfiles.com).

Character optimization is often performed following the proposal of De Pinna (1991), which argued that ACCTRAN is preferable to DELTRAN because it preserves the hypotheses of primary homology. However, Agnarsson & Miller (2008) argue that they do not see theoretical components that make ACCTRAN more preferable than DELTRAN. Amorim (2002) argues that it is more reasonable to analyze the evolution of the characters case by case and to explicitly explain the reason for using ACCTRAN or DELTRAN rather than using only one optimization for all characters. Thus, in some cases (e.g., when there are terminals with non-observable or inapplicable state) ACCTRAN would consider it a spurious synapomorphy, whereas DELTRAN does not perform this transformation, considering an apomorphy for the taxa that have the given state only. Thus, in this case it is safer to adopt the latter. The preference of each optimization was explicitly indicated in the character list.

On homoplasy and apomorphy

Following from the conclusion of chapter 1, we will state the view of homoplasy in a more optimistic fashion (e.g., Assis, 2009, 2013; Franz, 2005), and not as a mere "…error in our preliminary assignment of homology while scoring the character matrix." (Nixon & Carpenter, 2011: 164). As, for instance, Wilkinson (1991) argued that homoplasy in sister group can be evidence of phylogenetic proximity as this trait evolved in the ancestor of these lineages. Thus, some homoplastic traits can be a reliable evidence of relationship (Assis, 2017). In addition, Franz (2005: 504) affirmed that: "Experience indicates that abundant yet informative homoplasy is as necessary as homology for reliable phylogenetic inference." In practice, homoplasies support the inference of monophyly, since they are apomorphies (Assis, 2017) as used by, for instance, Cerretti et al. (2014) in which they argued for "homoplasious apomorphies" as indicatives of characters states supporting some groups; and we will use this argumentation scheme as well.

Illustration

Most characters were illustrated using photographs and line drawings to facilitate identification of different character states. The photographs were taken with a Leica DFC420 digital camera coupled to a Leica MZ16 stereomicroscope. The images were obtained through the software LAS V4.1, then stacked in the software Helicon Focus 5.3.14 and edited in the software Adobe Photoshop CS6 and Adobe Illustrator CS6. In addition, drawings were made using the Leica DM2500 optical microscope with its coupled camera. Subsequently, these drawings were vectored and edited in Adobe Illustrator CS6 software.

Table 1. List of Dexiinae species included in the analysis, including information of their biogeographical distribution and the number of species included in each genus (all directly examined; asterisk indicates the type species).

Taxon	No. of species in genus	Biogeographic Region	Tribe
Aldrichiopa Guimarães, 1971	1	NT	Voriini
Aldrichiopa coracella (Aldrich, 1934)*			
Allothelaira Villeneuve, 1915	3	OR/AU/AF	Voriini
Allothelaira diaphana Villeneuve, 1915*			
Alpinoplagia Townsend, 1931	1	NT	Voriini
Alpinoplagia boliviana Townsend, 1931*			
Arrhinactia Townsend, 1927	2	NT	Voriini
Arrhinactia cylindrica Townsend, 1927*			
Ateloglossa Coquillett, 1899	14	NE/NT	Dexiini
Ateloglossa marginalis (Curran, 1924)			
Ateloglutus Aldrich, 1934	6	NT	Voriini
Ateloglutus (Proteloglutus) chilensis Brèthes, 1920*			
Ateloglutus (Ateloglutus) ruficornis Aldrich, 1934*			
Athrycia Robineau-Desvoidy, 1830	5	NE/NT/PA	Voriini
Athrycia cinerea (Coquillett, 1895)			
Beskia Brauer & Bergenstamm, 1889	1	NE/NT	Epigrimyiini
Beskia aelops (Walker, 1849)*			
Billaea Robineau-Desvoidy, 1830	74	NE/NT/PA/OR/AF	Dexiini
Billaea claripalpis (van der Wulp, 1895)			
Billaea lata (Macquart, 1849)			
Billaea menezi (Guimarães, 1977)			
Billaea minor (Villeneuve, 1913)			
Billaea rhynchophorae (Guimarães, 1977)			
Billaea rutilans (Fabricius, 1781)			
Blepharomyia Brauer & Bergenstamm, 1889	6	NE/PA	Voriini
Blepharomyia pagana (Meigen, 1824)			
Campylocheta Rondani, 1859	48	NE/NT/PA/OR/AF	Voriini
Campylocheta lipernis (Reinhard, 1952)			
Campylocheta praecox (Meigen, 1824)*			
Campylocheta townsendi (Smith, 1916)			
Chaetogyne Brauer & Bergenstamm, 1889	3	NT	Dexiini
Chaetogyne analis Curran, 1937			
Chaetogyne vexans (Wiedemann, 1830)*			
Chaetotheresia Townsend,1931	1	NT	Dexiini
Chaetotheresia crassa (Wiedemann, 1830)*			
Chetoptilia Rondani, 1862	6	PA/OR/AF	Dufouriini
Chetoptilia puella (Rondani, 1862)*			
Chrysopasta Brauer & Bergenstamm, 1889	1	AU	Rutiliini
Chrysopasta elegans (Macquart, 1846)*			
Cordyligaster Macquart, 1844	9	NE/NT	Sophiini
Cordyligaster petiolata (Wiedemann, 1830)*			

Cordyligaster tipuliformis Walker, 1858			
Cyrtophleba Rondani, 1856	11	NE/NT/PA	Voriini
Cyrtophleba ruricola (Meigen, 1824)*			
Cyrtophleba nigripalpis (Aldrich, 1926)			
Cyrtophleba sp			
Daetaleus Aldrich, 1928	2	NT	Dexiini
Daetaleus purpureus Aldrich, 1928*			
Dasyuromyia Bigot, 1885	9	NT	Dexiini
Dasyuromyia inornata (Walker, 1836)*			
Dexia Meigen, 1826	50	NE/PA/AF/OR	Dexiini
Dexia fulvifera von Röder, 1893			
Dexia rhodesia (Curran, 1941)			
Dexia rustica (Fabricius, 1775)*			
Dexia uelensis van Emden, 1954			
Dexia vacua (Fallén, 1817)			
Dexia varivittata Curran, 1927			
Dexiomimops Townsend, 1926	8	PA/OR	Voriini
Dexiomimops sp			
Diaugia Perty, 1833	1	NT	Dexiini
Diaugia angusta Perty, 1833			
Dinera Robineau-Desvoidy, 1830	28	NE/PA/OR/AF	Dexiini
Dinera ferina (Fallén, 1817)			
Dinera grisescens (Fallén, 1817)			
Doleschalla Walker, 1861	11	OR/AU	Doleschaliini
Doleschalla consobrina Bigot, 1888			
Doleschalla elongata (van der Wulp, 1885)			
Dufouria Robineau-Desvoidy, 1830	6	NE/PA	Dufouriini
Dufouria chalybeata (Meigen, 1824)			
Epigrimyia Townsend, 1891	2	NE	Epigrimyiini
Epigrimyia illinoensis Robertson, 1901			
Eriothrix Meigen, 1803	16	NE/PA	Voriini
Eriothrix rufomaculata (De Geer, 1776)*			
Estheria Robineau-Desvoidy, 1830	38	NE/PA/AF/OR	Dexiini
Estheria bohemani (Rondani, 1862)			
Estheria cristata (Meigen, 1826)			
Estheria picta (Meigen, 1826)			
Euanthoides Townsend, 1931	1	NT	Sophiini
Euanthoides petiolata Townsend, 1931*			
Eudexia Brauer & Bergenstamm, 1889	4	NT	Dexiini
Eudexia lopesi sp. nov.			
Eulasiona Townsend, 1892	12	NE/PA	Voriini
Eulasiona comstocki Townsend, 1892*			
Euoestrophasia Townsend, 1892	7	NT	Oestrophasiini
Euoestrophasia plaumanni Guimarães, 1977			
Euthera Loew, 1866	13	NE/NT/PA/OR/AF/AU	Eutherini
Euthera (Euthera) barbiellini Bezzi, 1925			
Euthera (Euthera) tuckeri Bezzi, 1925			
Formosia Guérin-Méneville, 1843	24	OR/AU	Rutiliini
Formosia heinronthi (Enderlein, 1936)			
Formosia solomonicola Baranov, 1936			
Freraea Robineau-Desvoidy, 1830	2	NE/PA	Freraeini
Freraea gagatea Robineau-Desvoidy, 1830*			
Geraldia Malloch, 1930	14	AU	Dexiini
Geraldia nuda Barraclough, 1992			

Goniochaeta Townsend, 1891	2	NE	Voriini
Goniochaeta plagioides Townsend, 1891*			
Halydaia Egger, 1856	5	PA/OR/AU	Voriini
Halydaia luteicornis (Walker, 1861)			
Heterometopia Macquart, 1846	4	AU	Dexiini
Heterometopia argentea Macquart, 1846*			
Hypovoria Villeneuve, 1913	5	NT/NE/PA	Voriini
Hypovoria cauta (Townsend, 1926)			
Hystrichodexia Röder, 1886	7	NT	Dexiini
Hystrichodexia echinata van der Wulp, 1891			
Kirbya Robineau-Desvoidy, 1830	9	NT/NE/PA	Voriini
Kirbya moerens (Meigen, 1830)*			
Leptothelaira Mesnil & Shima, 1979	5	PA/OR	Voriini
Leptothelaira longicauda Mesnil & Shima, 1979*			
Microchaetina van der Wulp, 1891	9	NT/NE	Voriini
Microchaetina petiolata (Townsend, 1919)			
Microsoma Macquart, 1855	2	PA	Freraeini
Microsoma exiguum Macquart, 1855*			
Minthoplagia Townsend, 1915	3	NT	Voriini
Minthoplagia rafaeli Townsend, 1915*			
Mochlosoma Brauer & Bergenstamm, 1889	18	NT/NE	Dexiini
Mochlosoma lacertosum (van der Wulp, 1891)			
Morphodexia Townsend, 1931	6	NT	Dexiini
Morphodexia barrosi (Brèthes, 1920)			
Myiomima Brauer & Bergenstamm, 1889	2	NT	Dexiini
Myiomima sarcophagina Brauer & Bergenstamm, 1889*			
Neoeuantha Townsend, 1931	2	NT	Sophiini
Neoeuantha aucta (Wiedemann, 1830)*			
Neomyostoma Townsend, 1935	1	NT	Dexiini
Neomyostoma ptilodexioides Townsend, 1935*			
Neosophia Guimarães, 1982	3	NT	Sophiini
Neosophia elongata Guimarães, 1982*			
Neozelia Guimarães, 1975	1	NT	Dexiini
Neozelia alini Guimarães, 1975*			
Oestrophasia Brauer & Bergenstamm, 1889	3	NE/NT	Oestrophasiini
Oestrophasia calva Coquillett, 1902			
Ophirodexia Townsend, 1911	1	NE	Dexiini
Ophirodexia pulchra Townsend, 1911*			
Paedarium Aldrich, 1926	3	NT	Voriini
Paedarium sp			
Parahypochaeta Brauer & Bergenstamm, 1891	2	NT	Voriini
Parahypochaeta genalis (Townsend, 1927)			
Parodomyiops Townsend, 1935	1	NT	Voriini
Parodomyiops thelairopods Townsend, 1935*			
Pelycops Aldrich, 1934	1	NT	Dexiini
Pelycops darwini Aldrich, 1934*			
Periscepsia Gistel, 1848	44	NT/NE/PA/AF/OR	Voriini
Periscepsia (Ramonda) helymus (Walker, 1849)			
Periscepsia (Ramonda) prunaria (Rondani, 1861)			
Periscepsia sp			
Philippodexia Townsend, 1926	4	OR	Dexiini
Philippodexia longipes Townsend, 1926*			

Phyllomya Robineau-Desvoidy, 1830	24	NT/NE/PA/OR	Voriini
Phyllomya volvulus Robineau-Desvoidy, 1830*			
Plagiomima Brauer & Bergenstamm, 1891	13	NT/NE	Voriini
Plagiomima spinolusa (Bigot, 1889)			
Platyrrhinodexia Townsend, 1927	1	NT	Dexiini
Platyrrhinodexia punctulate Townsend, 1927*			
Polygaster van der Wulp, 1890	3	NT	Voriini
Polygaster brasiliensis Townsend, 1917			
Polygaster sp			
Polygastropteryx Mesnil, 1953	1	OR	Voriini
Polygastropteryx bicoloripes Mesnil, 1953*			
Prodiaphania Townsend, 1927	19	AU	Rutiliini
Prodiaphania victoriae (Malloch, 1936)			
Prophorostoma Townsend, 1927	2	NT	Dexiini
Prophorostoma pulchra Townsend, 1927*			
Prosena Lepeletier & Serville, 1828	28	NE/PA/OR/AU	Dexiini
Prosena siberita (Fabricius, 1775)*			
Prosenina Malloch, 1930	2	AU	Dexiini
Prosenina sandemani Barraclough, 1992			
Prosenoides Brauer & Bergenstamm, 1891	12	NE/NT	Dexiini
Prosenoides curvirostris (Bigot, 1889)*			
Prosenoides flavipes Coquillett, 1895			
Prosenoides haustellata (Townsend, 1927)			
Prosopochaeta Macquart, 1851	5	NT	Voriini
Prosopochaeta nitidiventris Macquart, 1851*			
Psecacera Bigot, 1880	7	NT	Dexiini
Psecacera chiliensis Bigot, 1880*			
Pseudodexia Brauer & Bergenstamm, 1891	1	NT	Voriini
Pseudodexia eques Brauer & Bergenstamm, 1891*			
Ptilodexia Brauer & Bergenstamm, 1889	45	NE/NT	Dexiini
Ptilodexia conjuncta (van der Wulp, 1891)			
Ptilodexia pacifica Wilder, 1979			
Ptilodexia sp			
Rasiliverpa Barraclough, 1992	2	AU	Dexiini
Rasiliverpa agrianomei (Mesnil, 1968)*			
Rhamphina Macquart, 1835	2	PA	Voriini
Rhamphina pedemontana (Meigen, 1824)*			
Rhamphinina Bigot, 1885	2	NY	Dexiini
Rhamphinina sp			
Rutilia Robineau-Desvoidy, 1830	57	OR/AU	Rutiliini
Rutilia (Grapholostylum) albovirida Malloch, 1929			
Rutilia (Chrysorutilia) caeruleata (Enderlein, 1936)			
Rutilia (Rutilia) setosa Macquart, 1847			
Rutilotrixa Townsend, 1933	8	AU	Dexiini
Rutilotrixa nigrithorax (Macquart, 1851)			
Sarcocalirrhoe Townsend, 1928	2	NT	Dexiini
Sarcocalirrhoe trivittata (Curran, 1925)			
Scotiptera Macquart, 1835	6	NT	Dexiini
Scotiptera sp			
Scotiptera venatoria (Fabricius, 1805)*			

Senostoma Macquart, 1847	29	AU	Dexiini
Senostoma longipes (Macquart, 1846)			
Spathidexia	25	NE/NT	Voriini
Spathidexia brasiliensis Arnaud, 1960			
Spathidexia dunningii (Coquillett, 1895)			
Spathidexia spatulate (Townsend, 1928)			
Stomina Robineau-Desvoidy, 1830	6	PA	Voriini
Stomina tachinoides (Fallén, 1817)			
Taperamyia Townsend, 1935	1	NT	Dexiini
Taperamyia sp			
Telothyria van der Wulp, 1890	43	NT/NE	Telothyriini
Telothyria itaquaquecetubae (Townsend, 1931)			
Telothyria rufostriata van der Wulp, 1890			
Thelaira Robineau-Desvoidy, 1830	19	NT/NE/PA/AF/OR/AU	Voriini
Thelaira americana Brooks, 1945			
Thelaira nigripes (Fabricius, 1794)			
Thelairaporia Guimarães, 1980	2	NT	Uramyini
Thelairaporia brasiliensis Guimarães, 1980*			
Thelairodes van der Wulp, 1891	4	NT	Voriini
Thelairodes vittigera (Bigot, 1889)			
Torocca Walker, 1859	5	PA/OR/AU	Doleschaliini
Torocca fasciata (Townsend, 1919)			
Torocca munda (Walker, 1856)			
Trafoia Brauer & Bergenstamm, 1893	9	NT/NE/PA	Voriini
Trafoia sp			
Trichodischia Bigot, 1885	2	NT	Voriini
Trichodischia soror Bigot, 1885*			
Trichodura Macquart, 1844	10	NT	Dexiini
Trichodura anceps (Fabricius, 1805)*			
Trichodura lineata Townsend, 1934			
Trichodura vidua Schiner, 1868			
Trixa Meigen, 1824	12	PA/OR	Dexiini
Trixa caerulescens Meigen, 1824			
Trixodes Coquillett, 1902	1	NE/NT	Dexiini
Trixodes obesus Coquillett, 1902*			
Tropidopsiomorpha Townsend, 1927	1	NT	Dexiini
Tropidopsiomorpha tropica Townsend, 1927*			
Uramya Robineau-Desvoidy, 1830	34	NE/NT	Voriini
Uramya fasciata (Macquart, 1848)			
Uramya halisidotae (Townsend, 1916)			
Uramya longa (Walker, 1853)			
Uramya producta Robineau-Desvoidy, 1830*			
Ushpayacua Townsend, 1928	1	NT	Dexiini
Ushpayacua ureophila Townsend, 1928*			

Voria Robineau-Desvoidy, 1830 *Voria aurescens* (Townsend, 1892) *Voria ruralis* (Fallén, 1810)	9	NT/NE/PA/AF/OR/AU	Voriini
Xanthodexia van der Wulp, 1891 *Xanthodexia sericea* (Wiedemann, 1830)	2	NT	Voriini
Yahuarmayoia Townsend, 1927 *Yahuarmayoia phaeoptera* (Wiedemann, 1830)	1	NT	Dexiini
Zelia Robineau-Desvoidy, 1830 *Zelia lateralis* (Townsend, 1919) *Zelia plumosa* (Wiedemann, 1830) *Zelia potens* (Wiedemann, 1830) *Zelia vertebrata* (Say, 1829)	23	NE/NT	Dexiini

Table 2. Species used as outgroup included in the analysis, including information of their biogeographical distribution.

Taxon	Tribe/Subfamily	Region
Archytas Jaennicke, 1867 *Archytas incertus* (Macquart, 1851)	Tachinini/Tachininae	NT/NE
Calliphora Robineau-Desvoidy, 1830 *Calliphora vomitoria* Linnaeus, 1758	Caliphorini/Calliphorinae	OR/AU/AF
Cholomyia Bigot, 1884 *Cholomyia inaequipes* Bigot, 1884	Myiophasiini/Tachininae	NT/NE
Eutrichopoda Townsend, 1908 *Eutrichopoda pyrrhogaster* (Wiedemann, 1830)	Trichopodini/Phasiinae	NT
Eutrixa Coquillett, 1897 *Eutrixa* sp	Palpostomatini/Tachininae	NE/NT
Imitomyia Townsend, 1912 *Imitomyia sugens* (Loew, 1863)	Imitomyiini/Phasiinae	NE/PA/AF
Irengia Townsend, 1935 *Irengia* sp	Megaprosoponi/Tachininae	NT
Lespesia Robineau-Desvoidy, 1863 *Lespesia lata* (Wiedemann, 1830)	Eryiini/Exoristinae	NT/NE/AU
Leucostoma Meigen, 1803 *Leucostoma aterrimum* Herting, 1971	Leucostomatini/Phasiinae	NT/NE/PA/AF
Palpostoma Robineau-Desvoidy, 1830 *Palpostoma pallens* (Curran, 1927)	Palpostomatini/Tachininae	AF/AU
Phasia Latreille, 1804 *Phasia* sp	Phasiini/Phasiinae	NT/NE/PA/AF/OR/AU
Uruleskia Townsend, 1934 *Uruleskia aurescens* Townsend, 1934	Leskiini/Tachininae	NT
Winthemia Robineau-Desvoidy, 1830 *Winthemia pinguis* (Fabricius, 1805)	Winthemiini/Exoristinae	NE/NT/PA/AF/OR/AU

3. Results

Phylogenetic analysis

We carried out a morphological phylogenetic analysis of the Dexiinae, including all currently valid and invalid tribes from all biogeographical regions. Our study included 150 species from 105 genera in the ingroup, in addition to 12 species in the outgroup. Our analysis included a total of 212 characters from the egg (2), first instar larva (30), adult external morphology (97, excl. terminalia), female terminalia (19), male terminalia (59) and spermatheca (2). The list of characters is presented in Appendix 1, with discussion of some characters and information on length, consistency index, retention index, and preferred optimization (ACCTRAN or DELTRAN, if any) for all characters. The data matrix is provided in Appendix 2.

The topologies obtained under implied weighting with different concavity values (K) show few changes regarding the number of most parsimonious trees (MPT). The analysis with k = 1-6 resulted in five MPT, while the analyses with the other k values resulted in three MTP; k = 10 onwards show the same three MTP as the equal weighed trees. As these k-values determines how strongly it weights against incongruent (homoplastic) characters, the decision to choose any of these trees in totally arbitrary, as long as the philosophy behind this methodology holds. Goloboff (1993; Goloboff et al., 2008; see also de Laet, 2015) connects this idea of weighting against homoplasy to the general ideas of Farris (1983) that argued that homoplasy is an *ad hoc* hypothesis because it cannot be explained by inheritance from a common ancestor. As a result, these procedures usually result in different topologies in relation to those obtained before the weighting, as it was the case of the present phylogenetic hypothesis. Relying on the discussion made in the Chapter 1, homoplasy as a process: 1) is not an error and it exists beyond trees; 2) can be due to evolutionary process, that can, in some cases, reflect evidence of the occurrence of adaptation, hence it is a source of important information about the operation of natural selection; 3) it is not always unreliable and can be informative in certain cases; 4) does not constitute an *ad hoc* hypothesis.

Hence, weighing against homoplasy can be problematic as we could have been down-weighting reliable information (that could support some clades) or some information about the process and history of certain taxa in relation to convergence and analogy (that can be due to adaptation). In this sense, one can lose this precioueses information about the history of our characters that could base additional research about its functions and evolution. If we are willing to disregard some of these patterns (traits that can confirm monophyletic groups) and process (homoplasy due to analogy and/or adaptation due to similar environmental and selective pressure), in order to weight them, thus it should be unproblematic to the cladistics that uses this type of reasoning. However, if we are trying to reflect, the best we can, the evolutionary history of the taxa that possess this character and if we want to develop the science of the phylogenetic as a causal one, we should maintain those homoplastic traits and put them to further test in order to know better its interaction (and function) in relation to other characters and its environment to get a fuller understanding of its history. Finally, based on these distinctions and discussions, we will only consider the equal-weighed trees for discussion.

The phylogenetic analysis with equal weights resulted in three most parsimonious trees (L = 1716; CI = 24; RI = 72) (Fig. 3). The implied weighting analysis resulted in a single tree with same length and topology as the equal weighting analysis, but with differences in the optimization of some characters. The single most parsimonious tree with equal weighting will be used in the discussion with unambiguous characters optimized and clades numbered (Fig. 3). Cladograms with ACCTRAN and DELTRAN character optimization and the Bremer index (1994) for each clade are provided in Appendix 3.

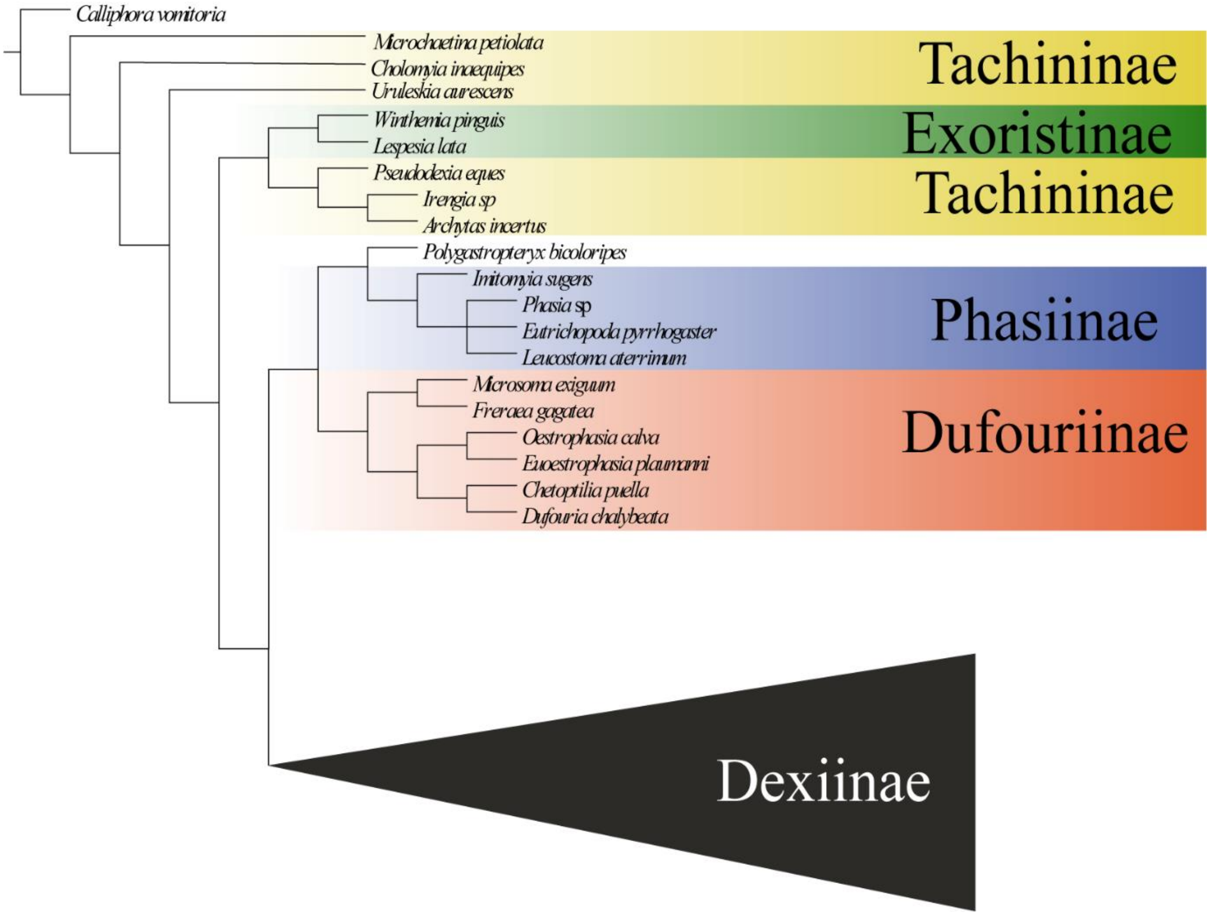


Figure 1. Phylogenetic tree from the strict consensus tree of three MTP showing the relationship of the subfamilies, with the dexiine clade collapsed.

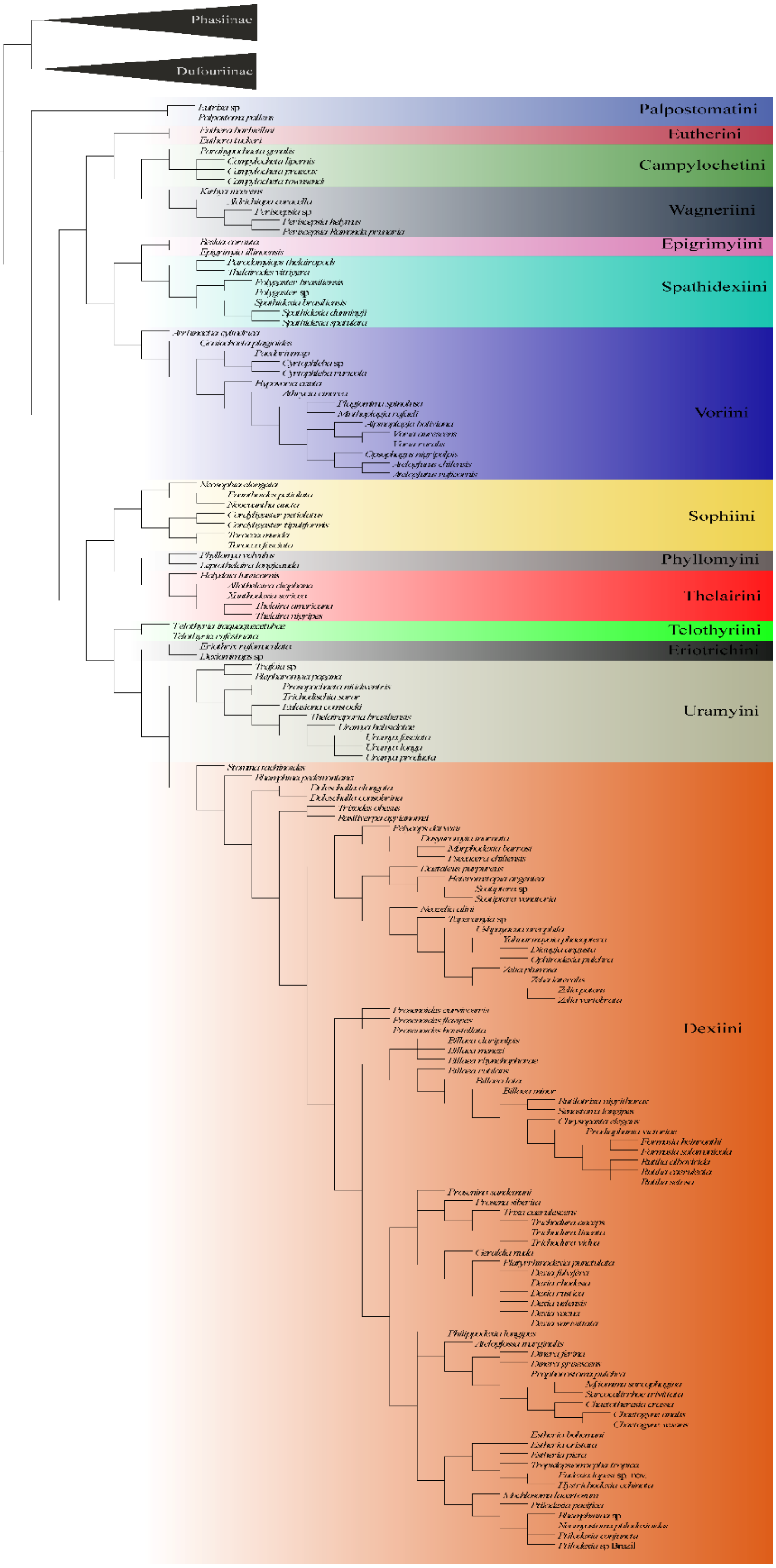
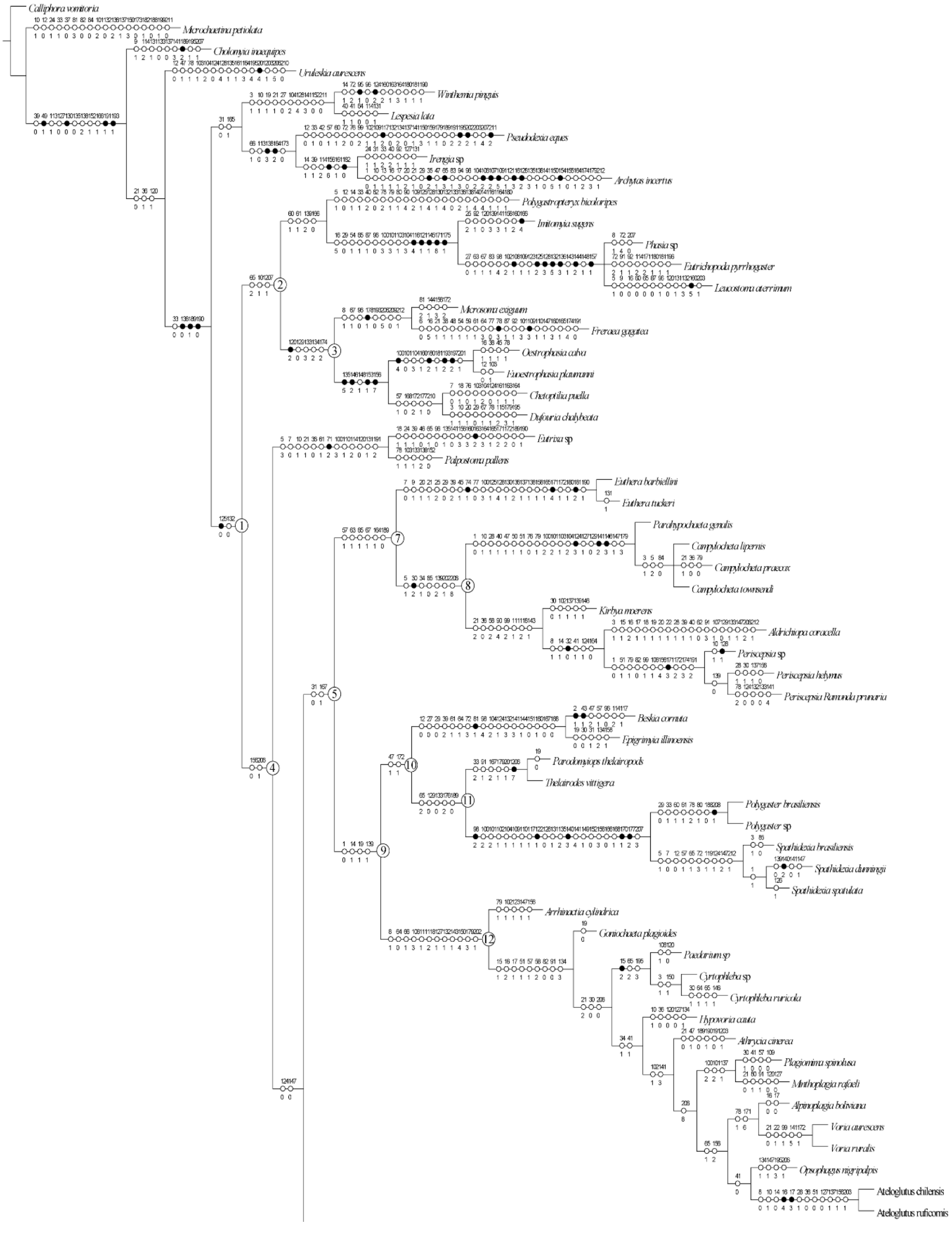


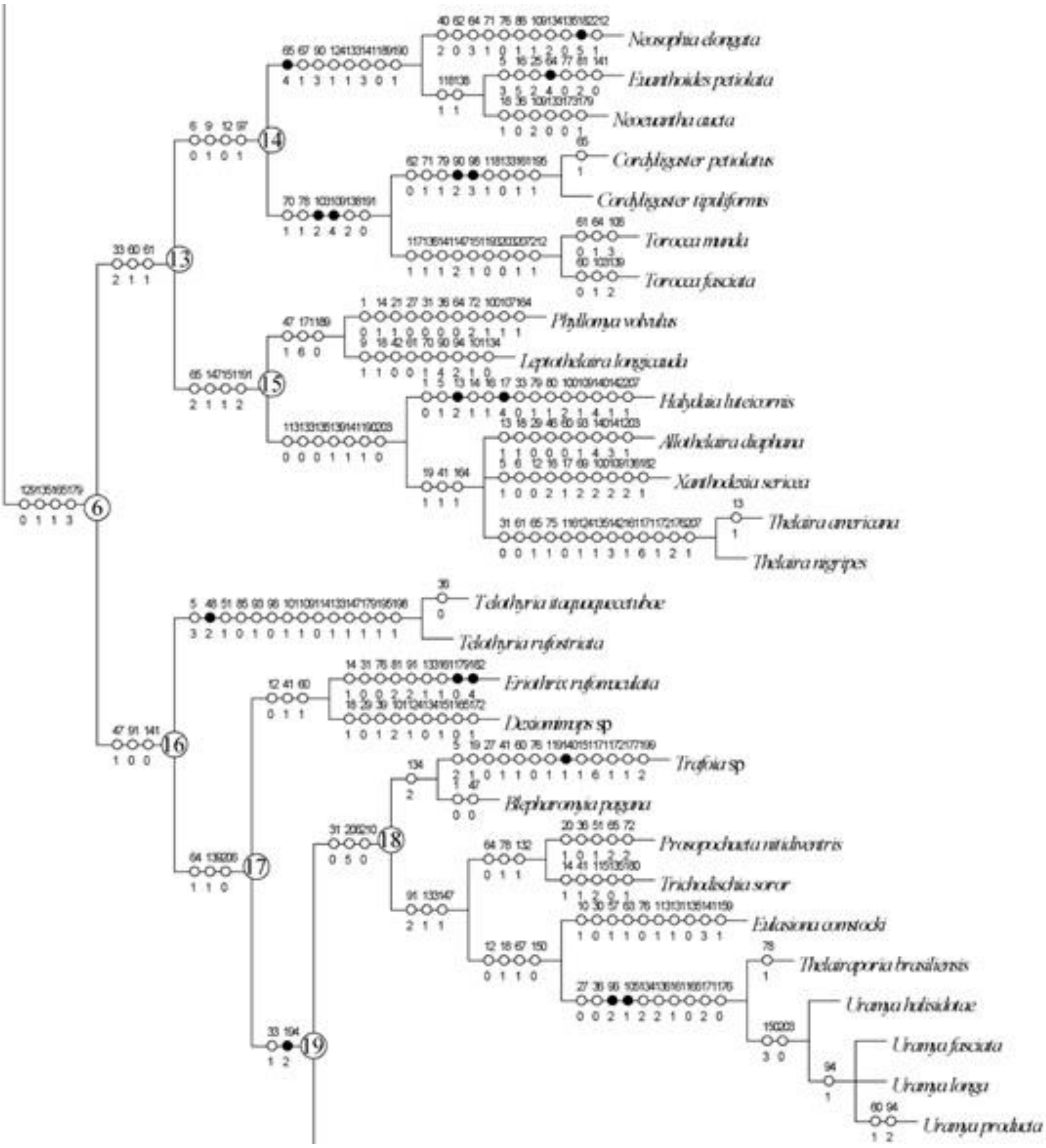
Figure 2. Phylogenetic tree from the strict consensus tree of three MTP showing the relationship of the dexiine tribes, with the dufouriine and phasiine clades collapsed.



(continued)

Figure 3. Strict consensus of the three most parsimonious trees under equal weights and unambiguous optimization.

(continued)



(continued)

Figure 3 (continuation). Strict consensus of the three most parsimonious trees under equal weights and unambiguous optimization.

(continued)

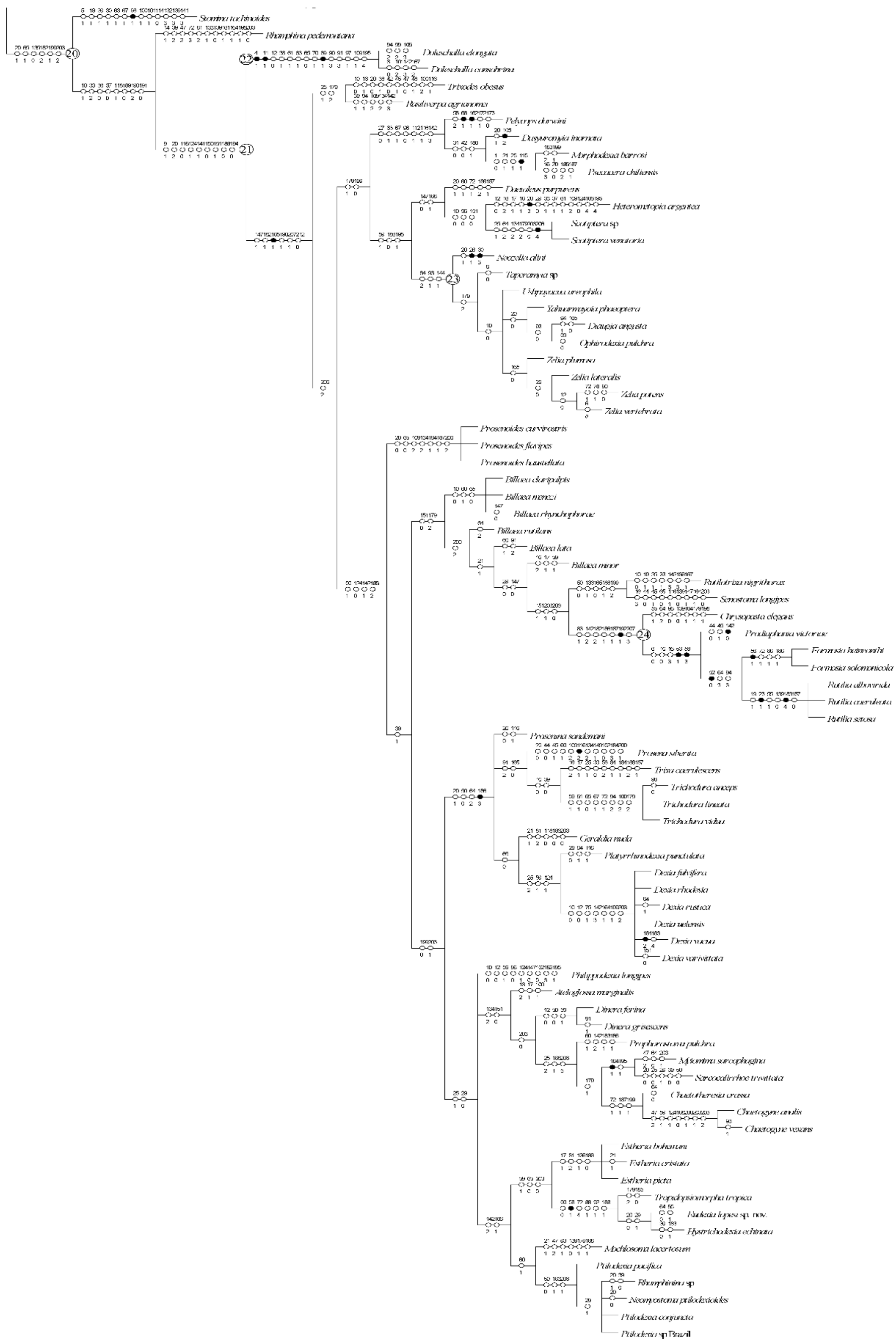


Figure 3 (continuation). Strict consensus of the three most parsimonious trees under equal weights and unambiguous optimization.

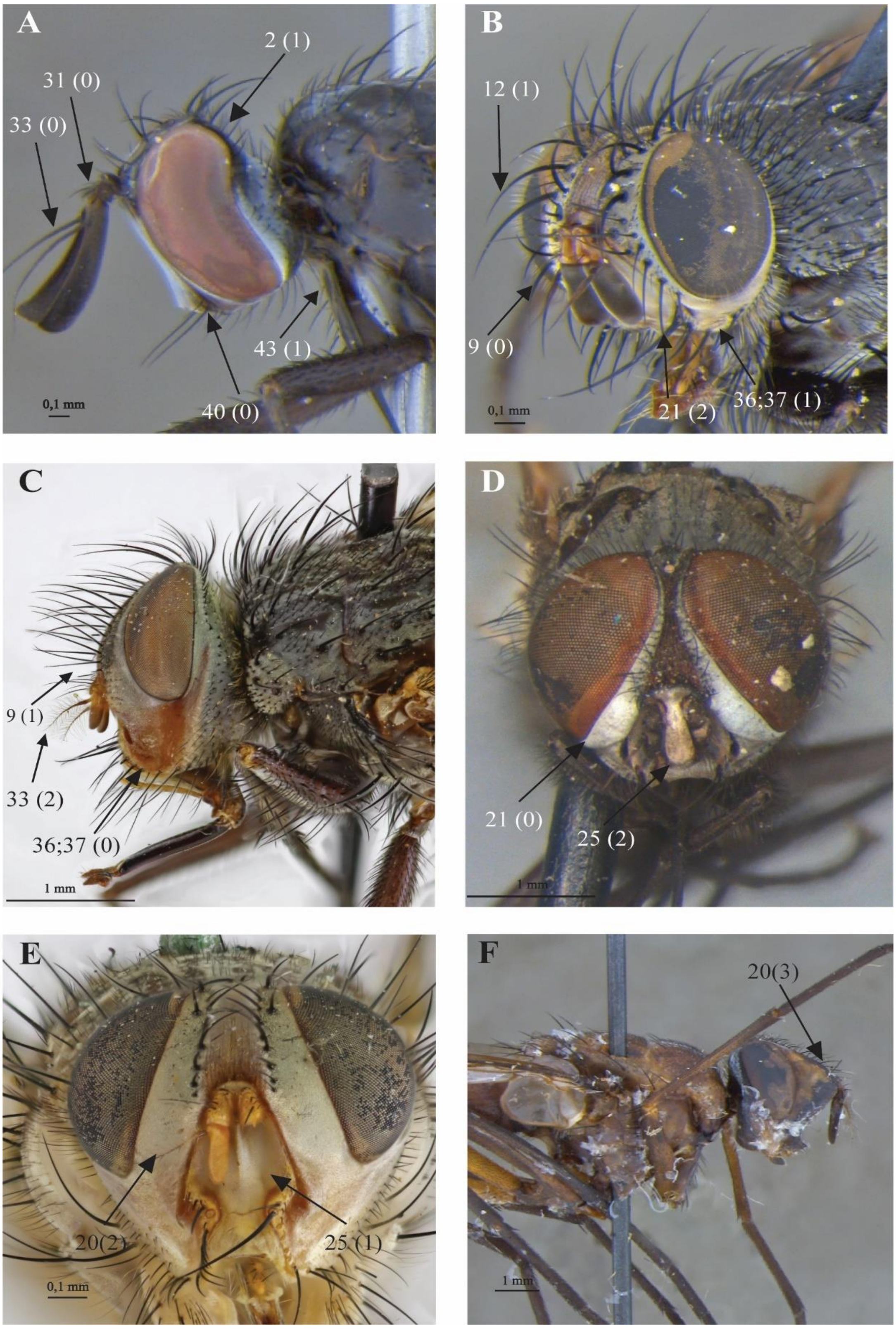


Figure 4. Head characters. A; *Beskia aelops* (Walker, 1849) ♂; B, *Cyrtophleba* sp ♂; C, *Rhamphinina discalis* (Townsend, 1915) ♂; D, *Imitomyia sugens* (Loew, 1863) ♂; *Ptilodexia rutilans* (van der Wulp, 1891) ♀; F, *Doleschalla elongata* (van der Wulp, 1885) ♀. The character number and its state (enclosed in parentheses) are pointed by arrows.

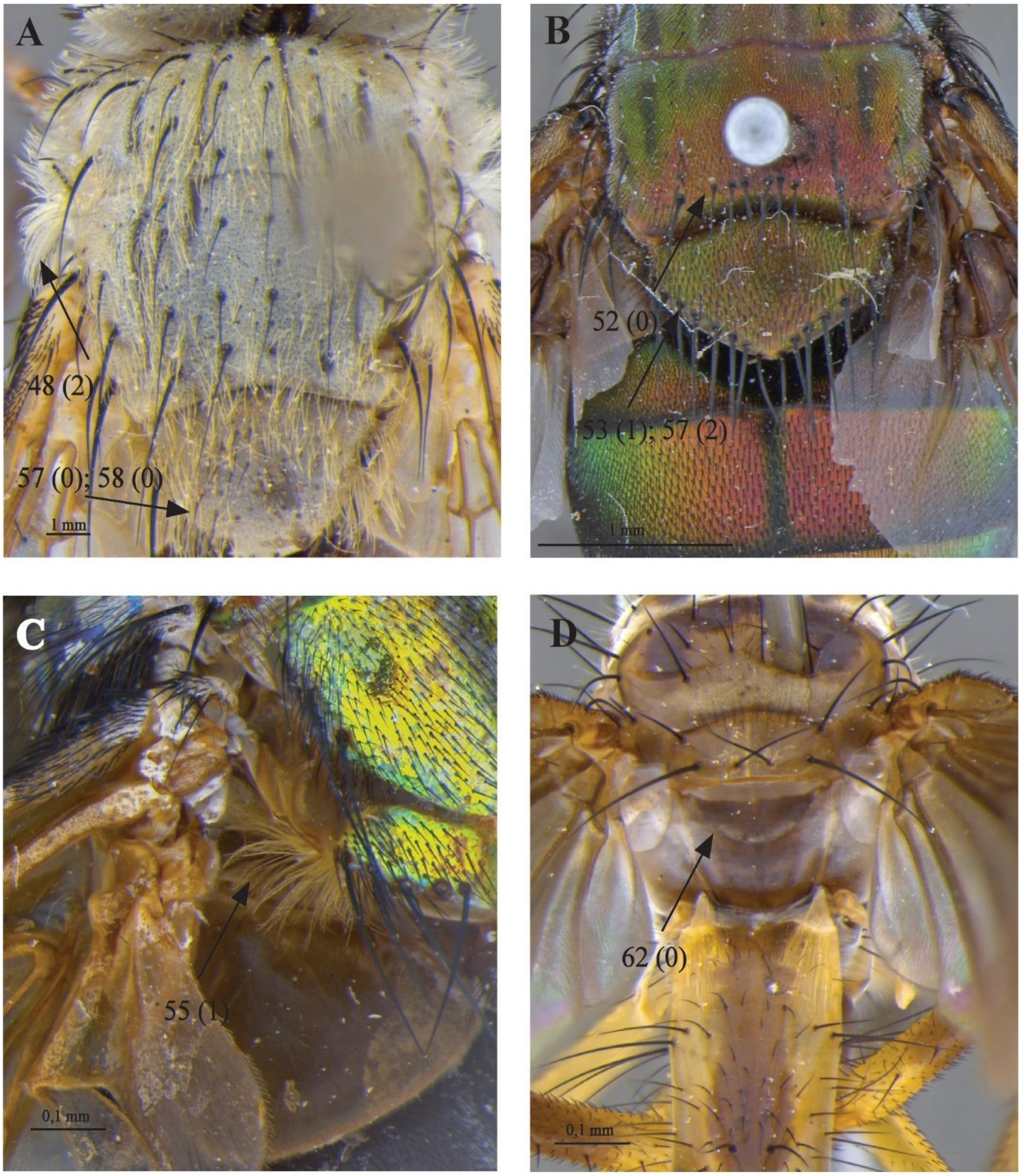


Figure 5. Thorax characters. A, *Telothyria rufostriata* van der Wulp, 1890 ♂; B; C, *Rutilia (Rutilia) setosa* Macquart, 1847 ♂; D, *Neosophia elongata* Guimarães, 1982 ♀. The character number and its state (enclosed in parentheses) are pointed by arrows.

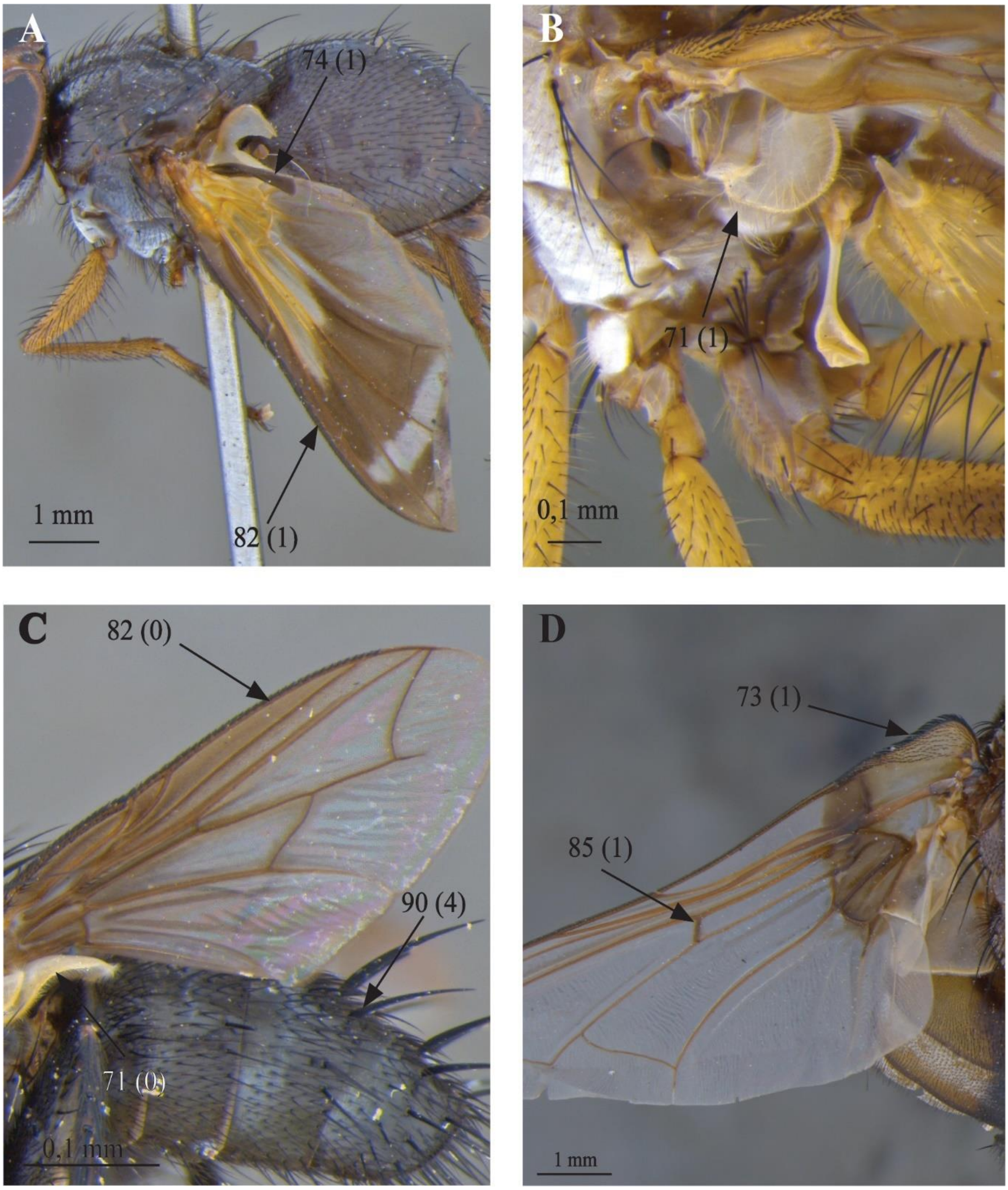


Figure 6. Wing characters. A, *Euthera (Euthera) barbiellini* Bezzi, 1925 ♂; B, *Neosophia elongata* Guimarães, 1982 ♀; C, *Cyrtophleba* sp ♂; D, *Prodiaphania victoriae* (Malloch, 1936) ♂. The character number and its state (enclosed in parentheses) are pointed by arrows.

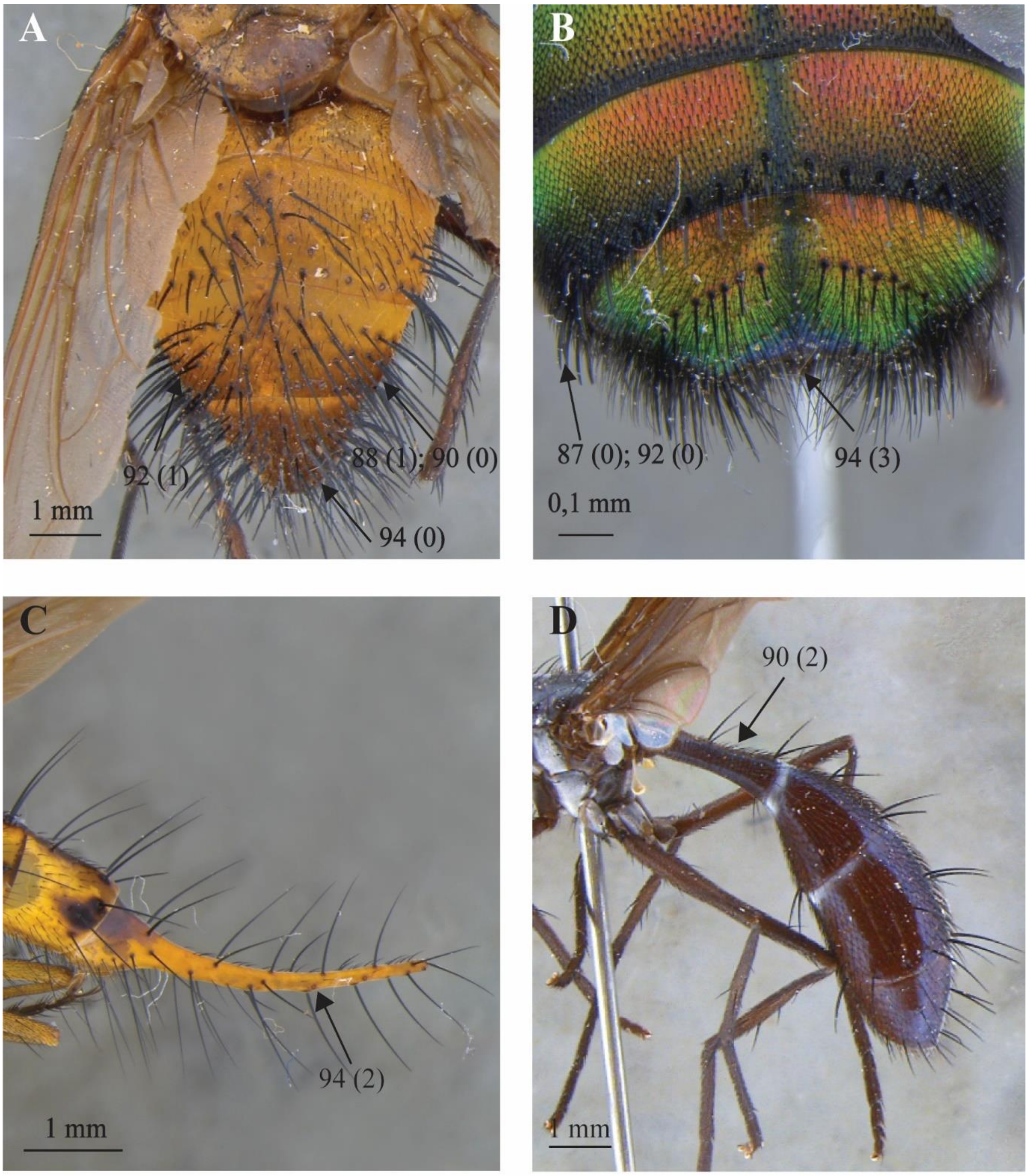


Figure 7. Abdomen characters. A, *Eudexia* colombiana (Townsend, 1929) ♂; B, *Rutilia (Rutilia) setosa* Macquart, 1847 ♂; C, *Trichodura anceps* (Fabricius, 1805) ♂; D, *Cordyligaster petiolata* (Wiedemann, 1830) ♂**.** The character number and its state are enclosed in parentheses and are pointed by arrows.

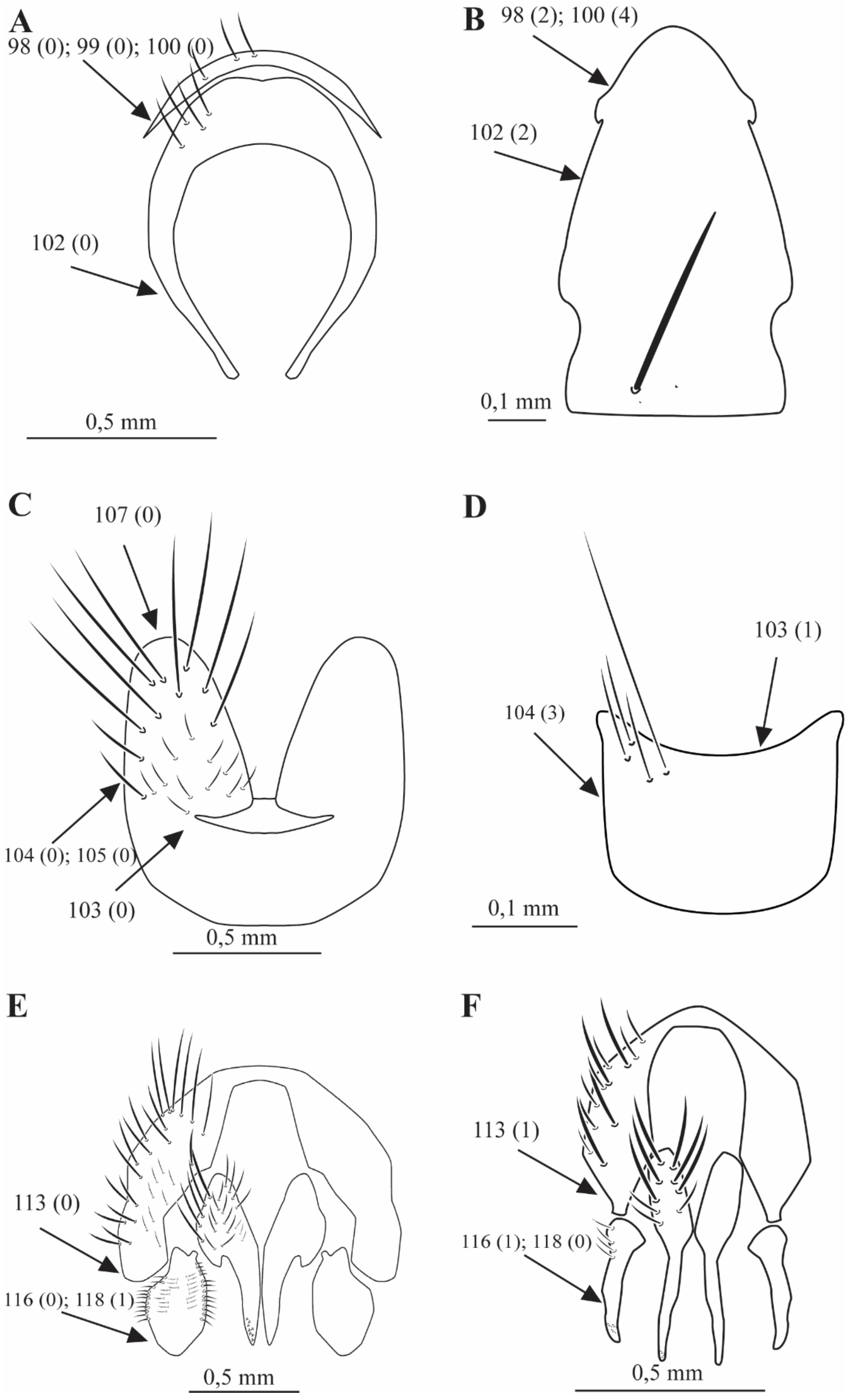


Figure 8. Male terminalia characters. A; F, *Sturmiodexia punctulata* (Townsend, 1927); B; D, *Euoestrophasia plaumanni* Guimarães, 1977; C; E, *Eudexia lopesi* **sp. nov**. The character number and its state (enclosed in parentheses) are pointed by arrows.

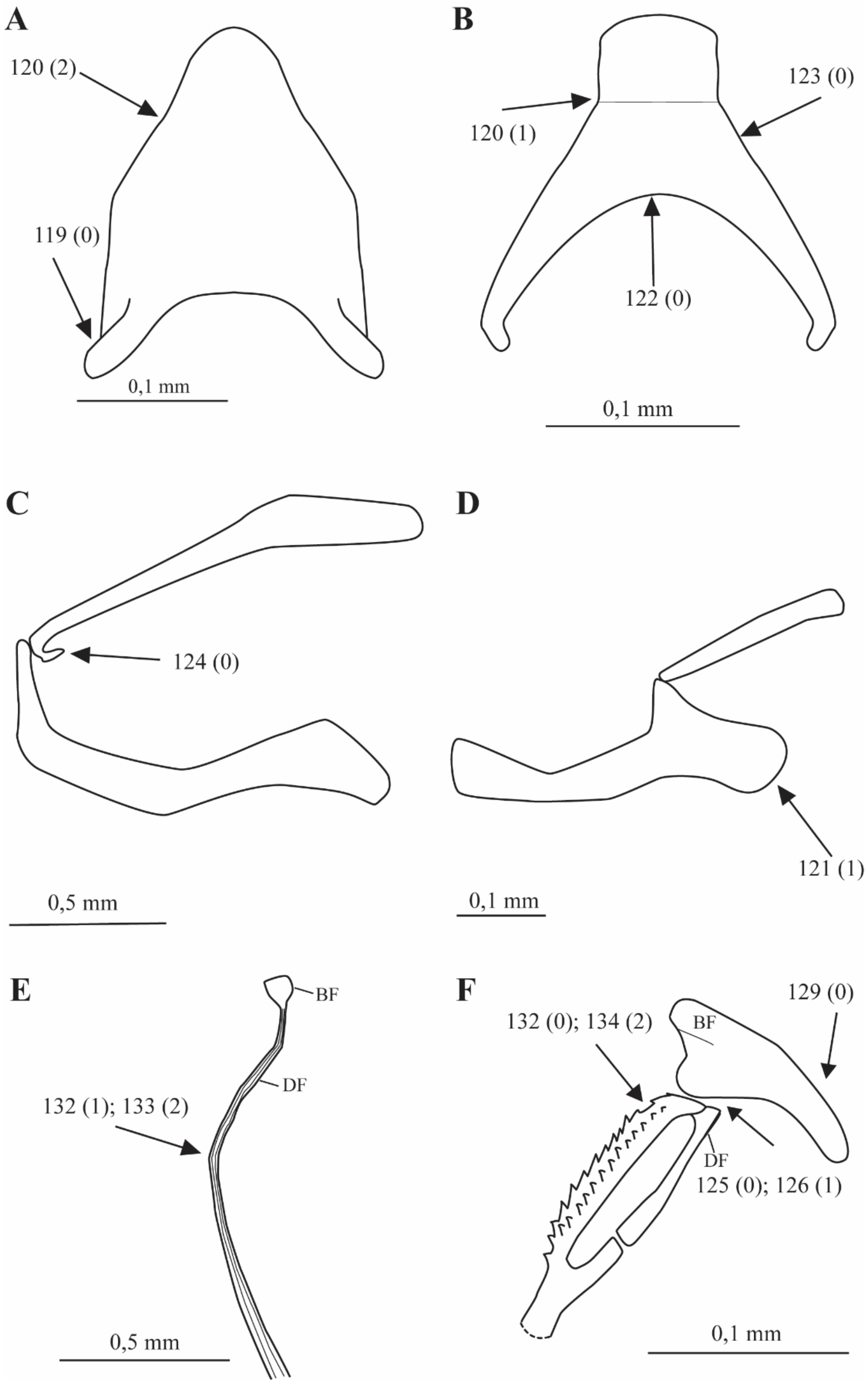


Figure 9. Male terminalia characters. A, *Euoestrophasia plaumanni* Guimarães, 1977; B; C, *Prophorostoma pulchra* Townsend, 1927; D, *Imitomyia sugens* (Loew, 1863); E, *Ateloglutus (Ateloglutus) ruficornis* Aldrich, 1934; F, *Dufouria chalybeata* (Meigen, 1824). The character number and its state (enclosed in parentheses) are pointed by arrows. (Legendas: *BF*, basiphallus; *DF*, distiphallus).

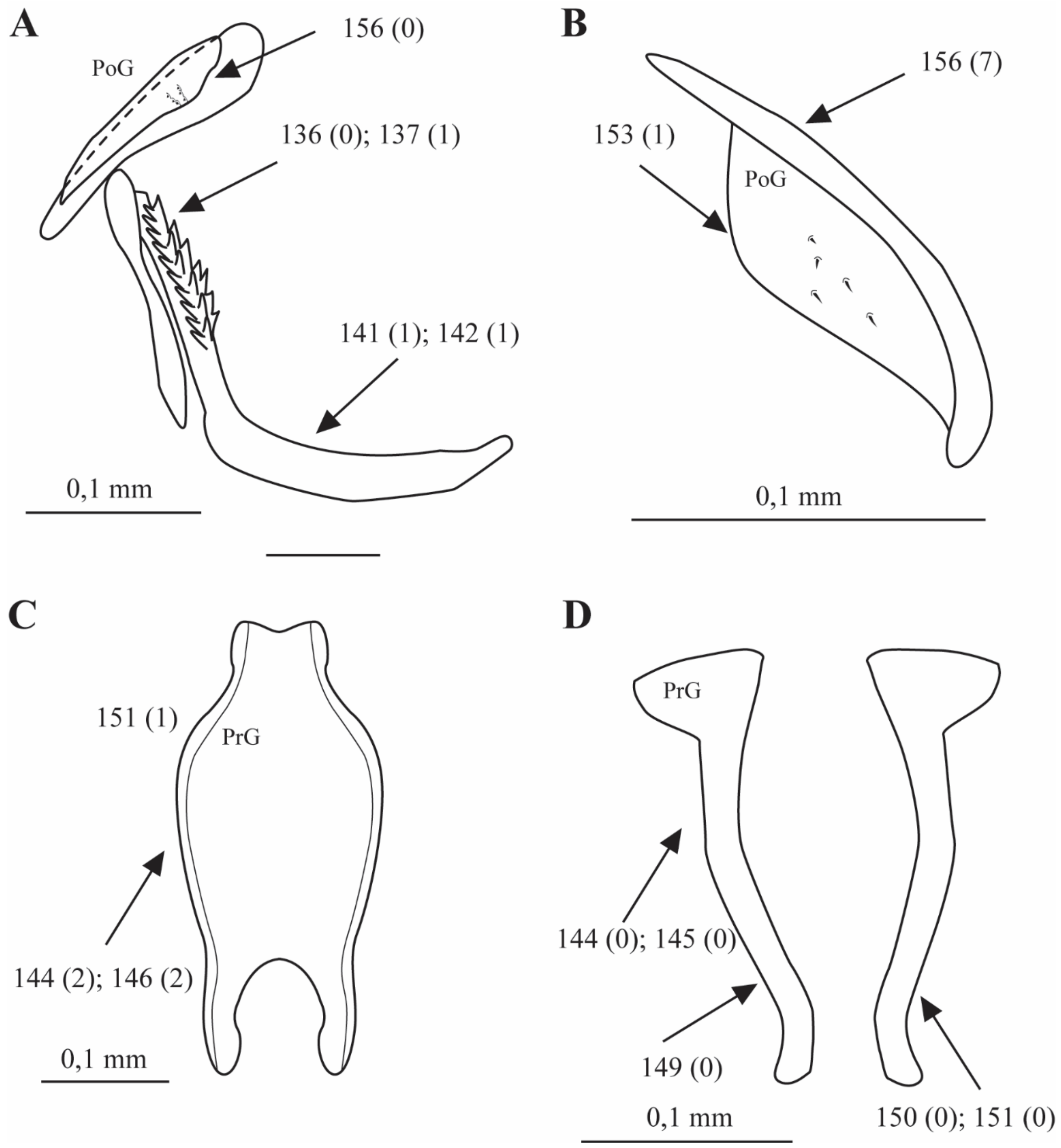


Figure 10. Male terminalia characters. A; D, *Prophorostoma pulchra* Townsend, 1927; B; C, *Euoestrophasia plaumanni* Guimarães, 1977. The character number and its state (enclosed in parentheses) are pointed by arrows. (Legendas: PoG: postgonite; PrG, pregonite).

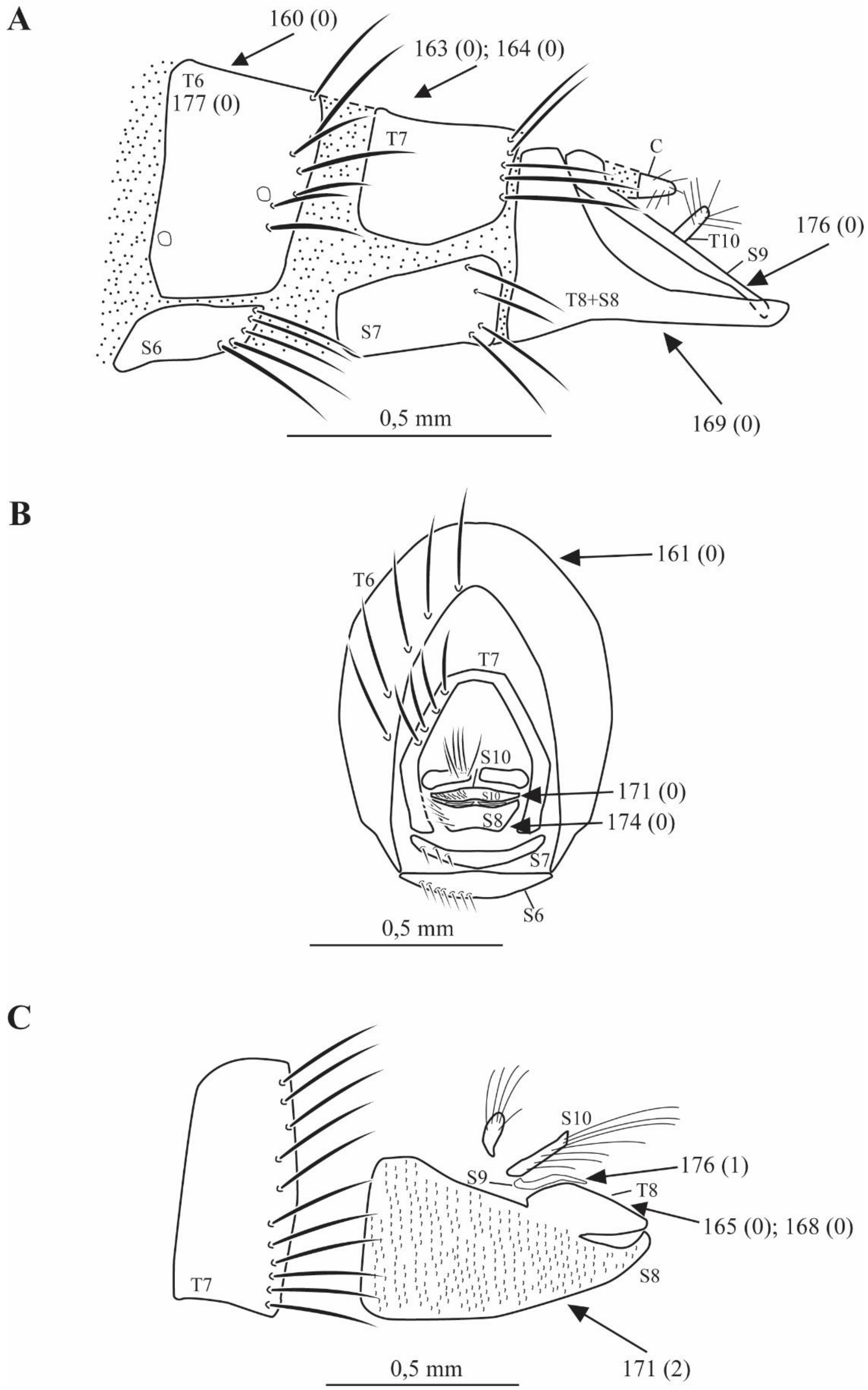


Figure 11. Female terminalia characters. A, *Dufouria chalybeata* (Meigen, 1824); B, *Sturmiodexia punctulata* (Townsend, 1927); C, *Uramya producta* Robineau-Desvoidy, 1830. The character number and its state (enclosed in parentheses) are pointed by arrows. (Legends: *C*, cercus; *S*, sternite; *T*, tergite).

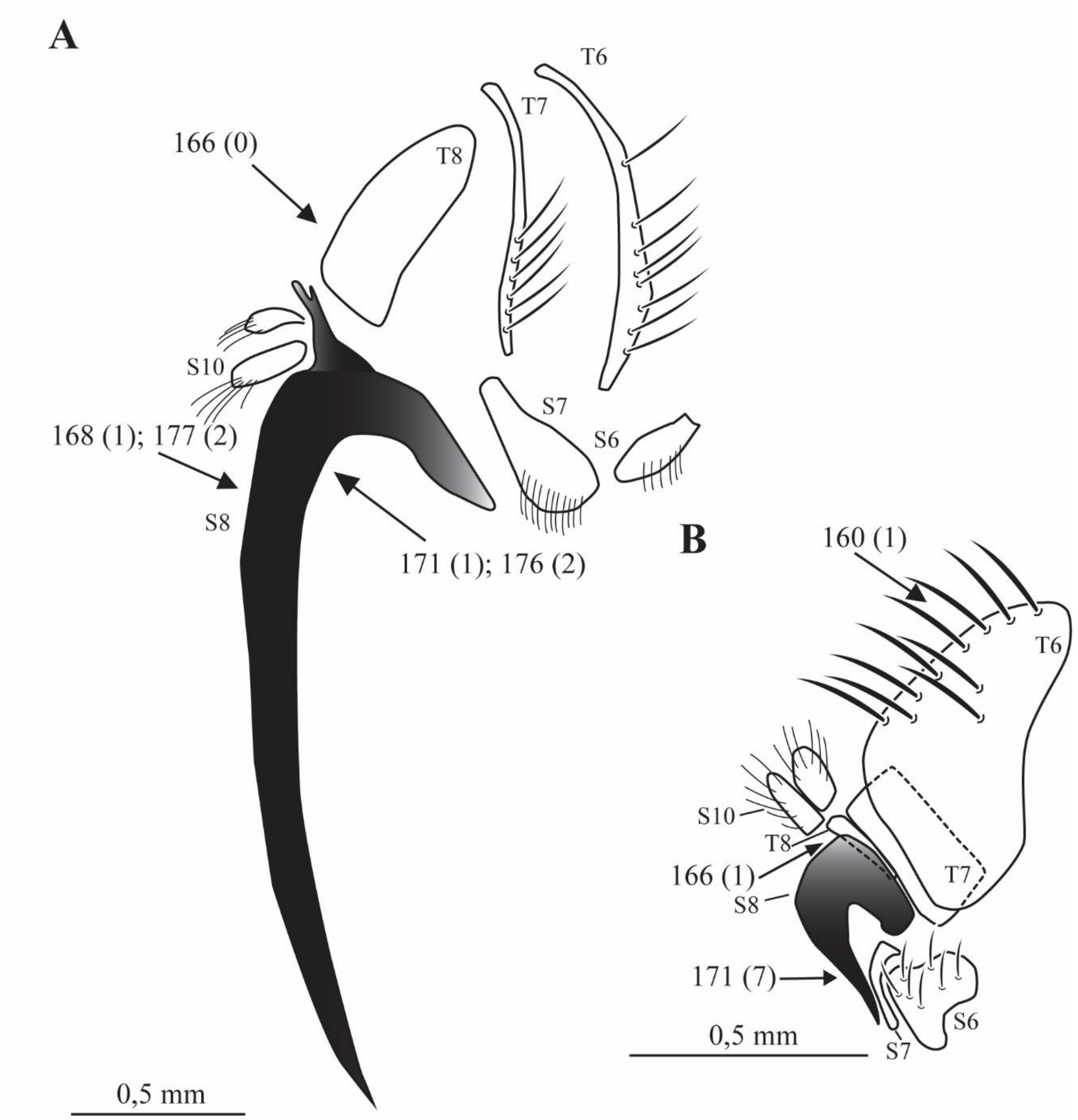


Figure 12. Female terminalia characters. A, *Polygaster* sp; B, *Beskia aelops* (Walker, 1849). The character number and its state (enclosed in parentheses) are pointed by arrows. (Legends: *C*, cercus; *S*, sternite; *T*, tergite).

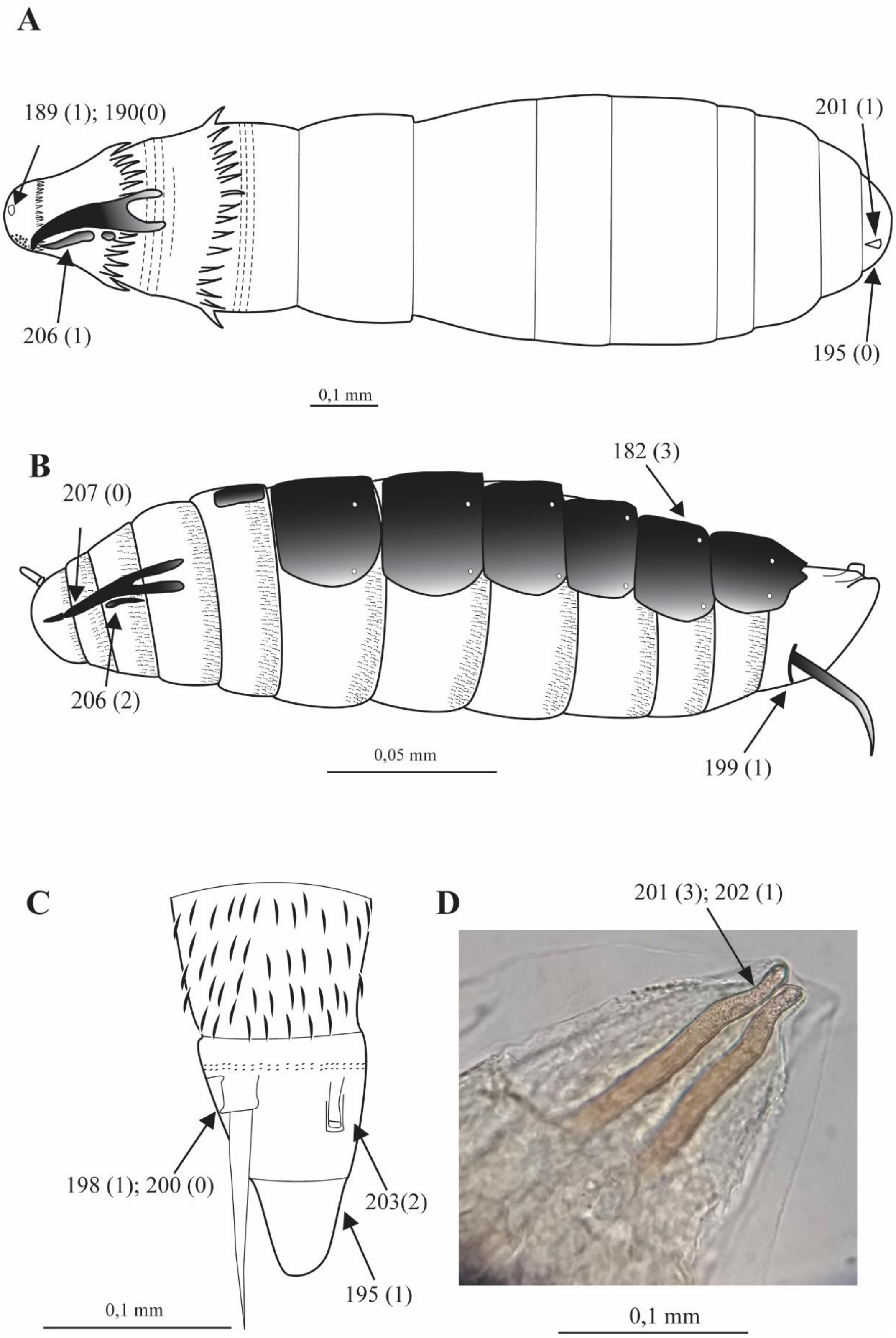


Figure 13. First instar larval characters. A, *Euoestrophasia plaumanni* Guimarães, 1977; B, *Neosophia bispinosa* de Santis & Nihei, 2019; C, *Euanthoides petiolata* Townsend, 1931; D, *Ateloglutus (Ateloglutus) ruficornis* Aldrich, 1934. The character number and its state (enclosed in parentheses) are pointed by arrows.

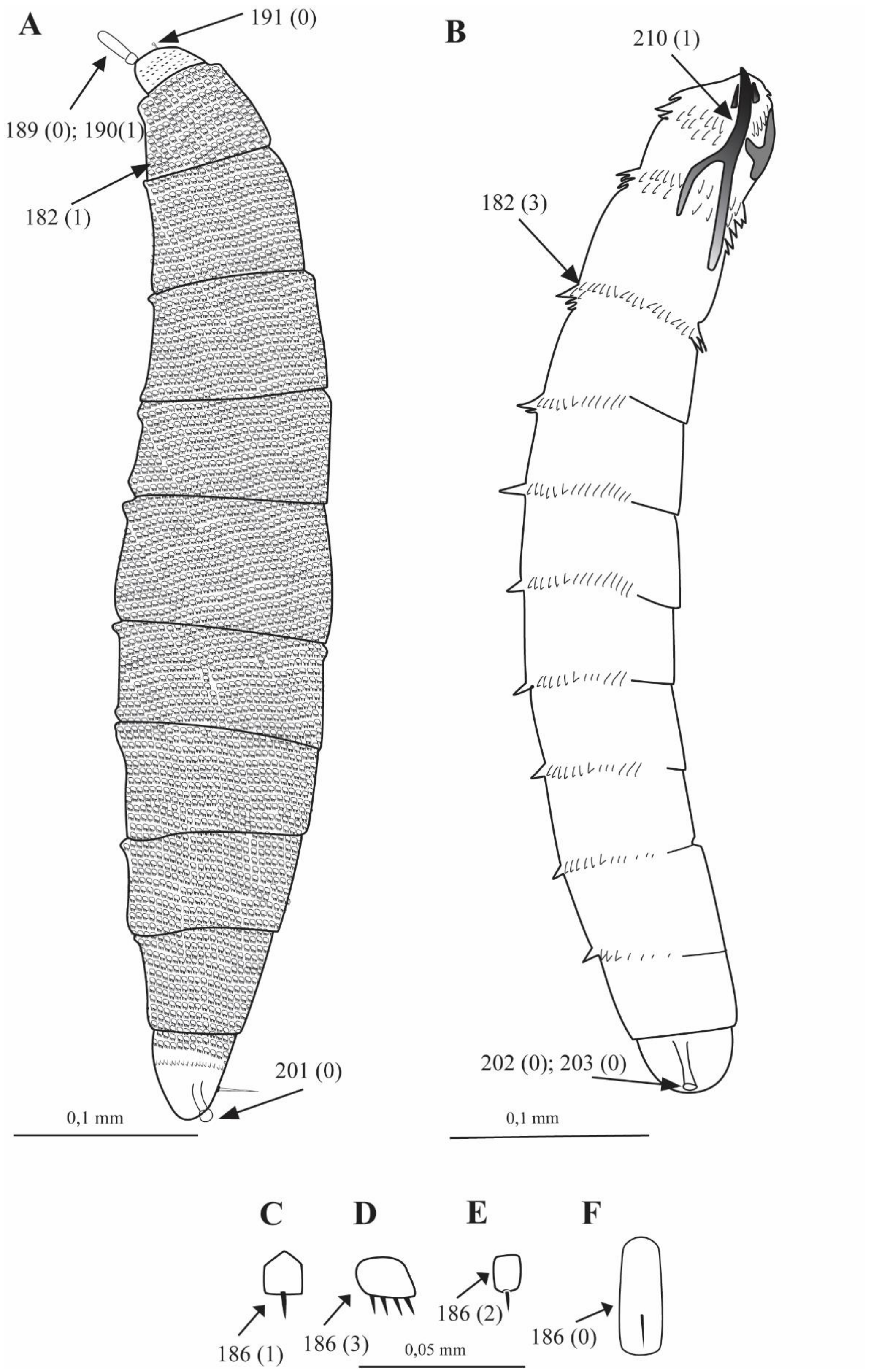


Figure 14. First instar larval characters. A; D, *Sturmiodexia punctulata* (Townsend, 1927); B, *Freraea gagatea* Robineau-Desvoidy, 1830; C, *Prophorostoma pulchra* Townsend, 1927; E, *Trichodura anceps* (Fabricius, 1805); F, *Rutilia (Rutilia) setosa* Macquart, 1847. The character number and its state (enclosed in parentheses) are pointed by arrows.

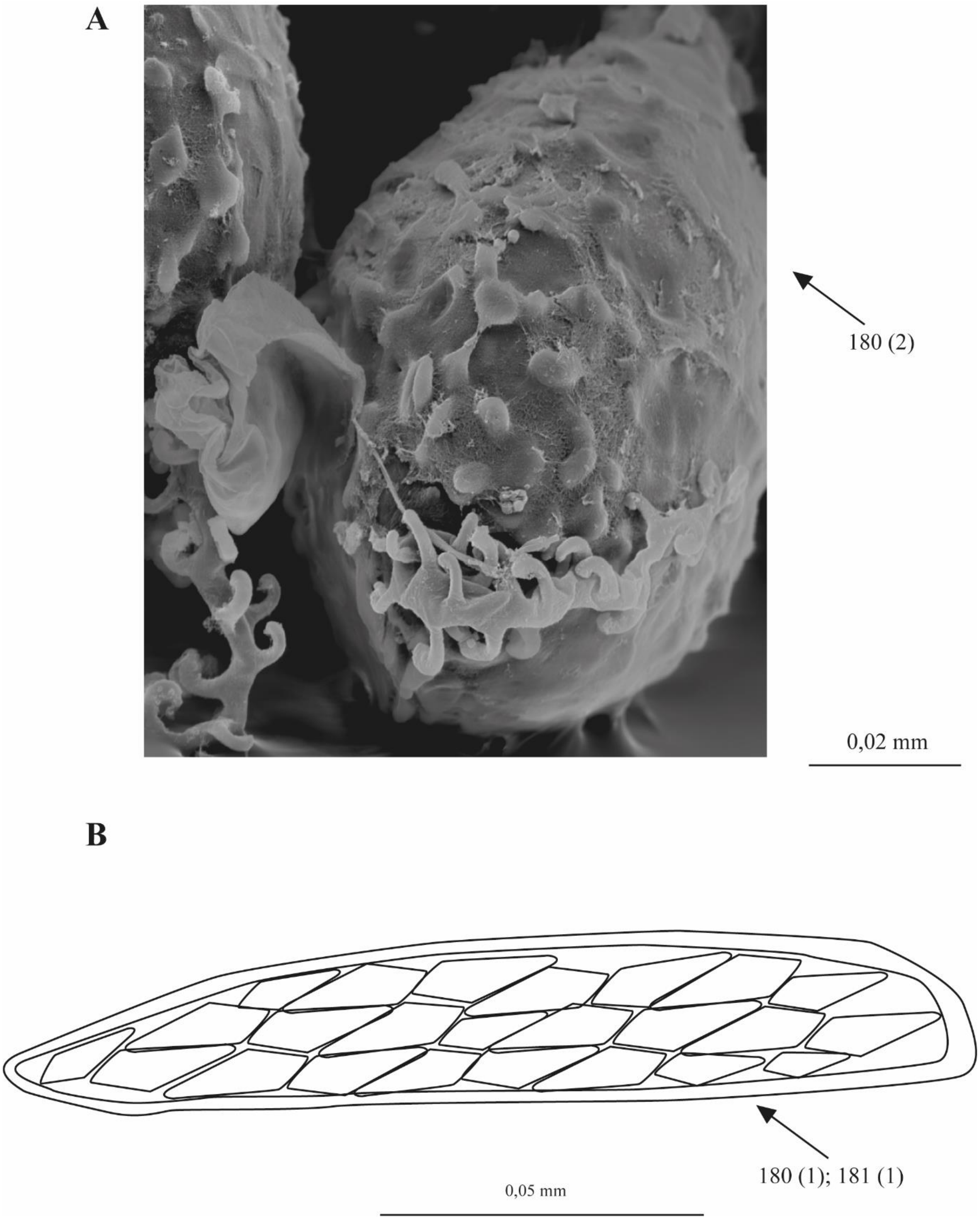


Figure 15. Egg characters. A, *Euoestrophasia plaumanni* Guimarães, 1977; B, *Trichodischia soror* Bigot, 1885. The character number and its state (enclosed in parentheses) are pointed by arrows.

Phylogenetic tree topology: clusting and outstanding results

The strict consensus of the 3 MPT resulted in a hyphotesis that Dexiinae are monophyletic; and it is sister to a monophyletic Phasiinae in addition to being sister to Dufouriini, Freraeini and Oestrophasiini. Not surprisingly, these three tribes (clade 3) were recoverd as monophyletic and do not pertain to neither Phasiinae or Dexiinae, thus are best placed as the subfamily Dufouriinae. A monophyletic Imitomyiini was conclusively recovered within Phasiinae and do not belong to Dexiinae. Within Dexiinae the tribes Campylochetini **tribe rev**., Dexiini, Epigrimyiin, Eutherini, Thelairini, Spathidexiini **tribe rev**, Wagneriini, **tribe rev**., Sophiini; Phyllomyini **tribe rev**., Eriotrichini **tribe rev**., Uramyini, Telothyriini and Voriini were recovered as monophyletic and well nested in this subfamily. The ambiguous Eutheriini was confirmed as Dexiinae and was, surpresinly, nested with Camplylochetini + Wagneriini. Another ambiguous taxa that was also supported as Dexiinae was Epigrimyiini that is nested with Spathidexiini whitin a larger clade that includes Voriini (clade 9). An interesting result, was the clustering (Sophiini (Philomyiini + Thelairini)) (clade 13), that were thought of being very close to the Voriini clade, but was recovered in a different place in the present phylogeny. A rather suprising result was the group (Telothyriini (Eriotrichini (Uramyini + Dexiini))) (clade 16), as a monophyletic Uramyini was recovered as sister to Dexiini. Dexiini are monophyletic and and the synonymy of two former valid tribes, Doleschaliini and Rutiliini **synn. nov.**, of an enlarged Dexiini.

4. Discussion

The present study is the most comprehensive morphological phylogenetic analysis of Dexiinae to date. Following the Hennigian argumentation that only monophyletic groups presents natural and ontological proprieties, the phylogenetic branching pattern obtained by the phylogenetic analysis will be used to establish a new and revised classification. However, while grouping by synapomorphy is not problematic, the appropriate rank for the any two clades in question it is. Thus, the ranking problem in systematics (Hamilton, 2014), is an open issue on the theoretical aspects of systematics. Although one should be clear that ranking is inevitably a subjective judgement, the systematist that uses a certain ranking scheme must use the one that best represents the peculiarities of the studied group as reflected by its synapomorphies. Hence, the most outstanding discovery of the present extensive morphological phylogenetic study is the hypothesis that Dufouriinae is separated from Dexiinae and is the sister taxon to the Phasiinae (fig. 1); the whole hypothesis is the following: (Dexiinae (Phasiinae +

Dufouriinae)). In relation to the tribes of Dexiinae and Dufouriinae, 13 where recognized on the former, and 3 on the later (see appendix 4 for the new classification scheme) – those tribes where based on already published family-group names as summarized in Sabrosky (1999).

4.1. The relationship of Dufouriini, Freraeini and Oestrophasiini in relation to Phasiinae and Dexiinae

For a long time Dufouriini was considered as a tribe or subtribe of Phasiinae. It was initially allocated as a subtribe in Phasiini by Mesnil (1939) and then as tribe of Phasiinae by Emden (1945; 1950) based mainly on chaetotaxy. Verbeke (1962; 1963) considered the tribe as a new subfamily, Dufouriinae, including Dufouriini and Macquartiini (the latter currently in Tachininae), based mainly on postgonites of the intermediate type (between the sensory and the connective) Type II, and distiphallus DEG subtype. For Verbeke, that subfamily would be the "dispersing center" of Tachinidae, with Dufouriini being a "bridge" for Dexiinae and Voriinae. Although Dufouriinae *sensu* Verbeke does not belong to Phasiinae, he noted similarities between the two groups on male postabdomen. Crosskey (1976; 1980) also considered Dufouriini as a subfamily, but containing the tribes Imitomyiini and Dufouriini, as these two would be excluded from Phasiinae and Dexiinae. Cantrell (1988) agreeing with Crosskey (1976; 1980) stated that (1988:147): "The affinities of the Dufouriinae appear to be intermediate between those of the Phasiinae and Dexiinae and deserve further study." Barraclough (1992) reports, considering the female terminalia modifications (elongated tergite 8 forming a dorsal lamellae) of Palearctic Dufouriini, which would not belong to Dexiinae. And he later affirms that (1992:1152): "[T]he Dufouriini belong in neither the Phasiinae or Dexiinae."

However, in contrast to those authors, Tschorsnig (1985) considered Dufouriini as a Dexiinae, and based his proposition on some putative synapomorphies derived from the male terminalia: the aedeagus with basiphallus and distiphallus articulated with each other. This feature (115: 1 of Cerretti et al. 2014), which for a long time was characteristic of Dexiinae, was not considered as a synapomorphic character in Cerretti et al. 2014 – it was a synapormophy for Dexiinae + Phasiinae (secondarily lost in Phasiinae). Tschorsnig (1985) also recognized a number of similarities between the male terminalia of Dufouriini and Phasiinae, reporting that only the pregonite and aedeagus would position it near Dexiinae; and later he showed further traits that are shared by those group as: sternite 5 without lobes and without lateral membranous line; membranous connection between sternite 5 and 6; tergite 6 fused to segment 7+8. Recently the molecular analysis of Tachinidae was conducted by Stireman et al.

(2018) and, one more time, Dufouriini was showed as a paraphyletic (forming two distinct clades). However, it was not recovered as close to Phasiinae, instead, it showed a relationship with a clade of Palpostomatini e some other voriine clades.

Santis & Nihei (submitted) conducted a phylogenetic analysis of Dufouriini, based on a comprehensive and detailed morphological study of adult and immatures stages (totalizing 185 characters), and their results supported a splitting Dufouriini *s.l.* into three strongly supported and closely related tribes (clade 5): Dufouriini *sensu stricto*, Oestrophasiini and Freraeini. Dufouriini *sensu lato* was supported by four unambiguous synapomorphies, including the male terminalia with hypandrial apodeme with boundary with the central plate indistinct (123:2 of Santis & Nihei, submitted). They have found the genera *Microsoma* and *Pandelleia* to form a clade with the Freraeini (*Freraea* + *Eugymnopeza*), supported by eight synapomorphies; they revalidated the tribe Oestrophasiini with the genera *Cenosoma*, *Euoestrophasia*, *Jamacaria* and *Oestrophasia* were grouped in a strongly supported clade defined by 19 unambiguous synapomorphies; and Dufouriini *sensu stricto* was composed only of *Rondania*, *Chetoptilia*, *Dufouria*, *Comyops* and *Ebenia*, and defined by three synapomorphies. Santis & Nihei (submitted) also found evidence of a proximity between the clade (Freraeini (Oestrophasiini+Dufouriini) and Phasiinae, as they were recovered as sister group: Dufouriinae + Phasiinae. But, as their taxonomic sampling were reduced, with five out of 12 Dexiine tribes (Dexiini, Voriini, Dufouriini, Freraeini and Oestrophasiini), they preferred not propose any conclusions at the subfamily level.

Herein (fig. 1), Dufouriini with its three closed related tribes Oestrophasiini and Freraeini, once again formed a clade (clade 3) sister group to Phasiinae (clade 2). Relying on our extensive sampling (163 species of Dexiinae) and 212 characters from the adult (including male and female terminalia) and immature stages, in addition to the inclusion of members of all Dexiinae tribes, we herein propose to revalidate the subfamily Dufouriinae from Dexiinae. Dufouriinae presents the synapomorphy of the male terminalia with the boundary of the hypandrial apodeme in relation to central plate indistinct (120: 2) – the same obtained by Santis & Nihei (submitted) - and the platiform pregonite medially expanded (150: 2), in DELTRAN, in addition to 7 apomorphic traits as listed above; one of them, is the male terminalia with basiphallus prolonged in relation to epiphallus (120: 0) that is traditionally considered as a putative synapomorphy of Dexiinae (Tschorsnig, 1985). The clade (clade 2) of Phasiinae + Dufouriinae presents the ambiguous synapomorphy of male terminalia with pregonite platiform, medially expanded (150: 2) in ACCTRAN, in addition to 6 apomorphic traits as listed above. What about the widely recognized putative synapomorphy of Dexiinae, male terminalia with connection between basiphallus (dorsal sclerite) and distiphallus membranous (character 125: 0)? Herein this character state was hypothesized as a synapomorphy of (Dexiinae (Phasiinae + Dufouriinae)) - clade 1 - in addition to 5 apomorphic traits as listed above; one of them, is the ambiguous trait of male terminalia with male terminalia with membranous connection between basiphallus (dorsal sclerite) and distiphallus, 180º movement capacity movable (126: 1), in ACCTRAN, a trait usually related and discussed to Dexiinae as well. This trait (basiphallus and distiphallus articulated each other) was almost the same as found in Cerretti et al. (2014) – supporting Dexiinae + Phasiinae. Hence, our findings are congruent with those previously proposed by Verbeke (1962, 1963), Crosskey (1976; 1980), Cantrell (1988) and Barraclough (1992), that Dufouriini is actually Dufouriinae, a separate subfamily, not included in Dexiinae or Phasiinae. Finally, Dufouriinae presents an important biological characteristic: they parasite the same hosts, always attacking adult beetles, unlike the other members of the Dexiinae tribes, which attacks mainly Lepidoptera or Coleoptera larvae. Accordingly, this was one of the reasons that led Crosskey (1976) and Barraclough (1992) to consider Dufouriini as a separate subfamily.

4.2. Imitomyiini nested within the phasiines

Imitomyiini (*Imitomyia* Townsend, *Proriedelia* Mesnil, and *Riedelia* Mesnil), similarly to Eutherini and Epigrimyiini (that will be discussed in the next section) are historically classified one time in Dexiinae and other in Phasiinae, e.g., Herting (1984); O'Hara & Wood (2004). This is the reflection of a confusing interpretation of their morphological traits: their taxa present the elongated central plate of hypandrium, as putative synapomorphy of the phasiines, as discussed by Tschorsnig (1985); at the same time, they present male terminialia with the membranous connection between the basiphallus and distiphallus (however, does not present trait of the distiphallus with 180º movement capacity movable). Cerretti et al. (2014) recovered this tribe within Phasiinae by their morphological traits, and this configuration was further suggested, even if somewhat uncertain, by the molecular evidence of Blaschke et al. (2018). Stireman et al. (2018), however, suggested a rather different hypothesis: *Imitomyia* is clustered to Palpostomatini in a clade distinct from both Dexiinae and Phasiinae, forming the following classification (*Imitomyia* + Palpostomatini) + (Dexiinae + Phasiinae). Further morphological evidence, in addition to Cerretti et al (2014) tends to contradict the hypothesis of Stireman et al. (2018); Santis & Nihei (submitted) recovered *Imitomyia* within Phasiinae (in a clade that included, in addition to *Imitomyia*, *Strongygaster*, *Catharosia* and *Cylindromyia*) and presented the synapomorphy of Tschorsnig (1985) hypandrium with central plate elongated

(124: 1 of Santis & Nihei) together to trait of the female terminalia of the sharp (and piercer) sternite 8 (172: 1 of Santis & Nihei) for the phasiines. Both synapomorphies were further confirmed by the present phylogenetic hypothesis (121: 1 and 171: 8) for *Imitomyia* and the taxa of Phasiinae sampled (*Eutrichopoda*, *Leucostoma* and *Phasia*). Following these evidences, Imitomyiini is conclusively transferred to Phasiinae.

4.3. Clade 4: tribal relationships of the subfamily Dexiinae

The first group that appears within Dexiinae is the Palpostomatini (*Palpostoma*, *Eutrixa*) that occupies a sister group position to all other Dexiinae. This branching pattern is somewhat similar to the DNA-based phylogeny by Stireman et al. (2018) that recovered one group of Palpostomatini (*Palpostoma*, *Eutrixopsis*) as sister group to Dexiinae + Phasiinae and other (*Eutrixa*, *Xanthobasis*) within Dexiinae. A rather different configuration was suggested by Cerretti et al. (2014), as Palpostomatini (*Ciala*, *Eutrixopsis*, *Melisoneura*) appeared as sister group for all the remaining Tachinidae. What could explain for such disparate hypothesis?

It appears that at this moment, the tribe Palpostomatini is a polyphyletic group that comprehends rather two different groups as discussed by Mesnil (1974): some taxa from the Australasian, Neartic, Afrotropical, Oriental and Neotropical, that corresponds to almost all genera of the tribe, and the New World group, called by Mesnil as the subtribe Eutrixariae, that presents the genera New World genera *Eutrixa*, *Eutrixoides*, *Xanthobasis* and *Isodotus*. These groups present some outstanding differences in the male terminalia (e.g., Richter, 1980), the most conspicuous is the membranous connection between basiphallus and distiphallus that occurs only in the subtribe Eutrixariae of Mesnil. While Cerretti et al. (2014) only used those genera with the sclerotized connection between the basiphallus and distiphallus, the present work used those members of Palpostomatini (Eutrixariae of Mesnil) that, as showed, presents a membranous connection between basiphallus and distiphallus. In addition, Stireman et al. (2018) included some of the genera (*Eutrixa*, *Xanthobasis*) with the connection between the basiphallus and distiphallus hinged and angled, and these genera appeared within the Dexiinae and not clustered with the other Palpostomatini. Hence, probably the present configuration of Palpostomatini might change considerably when more taxa are added for a phylogenetic analysis of the whole tribe. Finally, for the reasons exposed, it is very premature to transfer this tribe, before this group become better known phylogenetically.

4.4. Eutheriini nested with Voriini

The phylogenetic position of Eutherini (*Euthera* Loew and *Redtenbacheria* Schiner) is complex and controversial. The members of this tribe present characters that are, traditionally, typical of Dexiinae like the platiform pregonite, but at the same time, does not present other typical traits like the hinged and angled connection between the basiphallus and distiphallus. Furthermore, they possess planoconvex eggs (Herting, 1966), that are typical of some members of Phasiinae and Exoristinae. Hence, although not conducting a phylogenetic analysis, some authors argued for their inclusion in Phasiinae (Guimarães, 1971; Crosskey, 1976; Herting, 1984) or Dexiinae (Verbeke, 1962; Tschorsnig, 1985; O'Hara & Wood, 2004; O'Hara et al., 2020). Finally, when the first phylogenetic hypothesis was conduct using morphological data, Cerretti et al. (2014) recovered, unexpectedly, this tribe within the subfamily Exoristinae. Only when the two DNA-based phylogenies were published, i.e., Blaschke et al. (2018) and Stireman et al. (2018), that Eutherini was suggested within the dexiines. Furthermore, both works recovered Eutherini clustered with Epigrimyiini, and this rather surprisingly result has not been suggested previously, and is derived from the genetic evidence only.

The inclusion of Eutheriini in Dexiinae was further confirmed by our phylogenetic hypothesis using morphological evidence (contra Cerretti et al., 2014). However, rather than sister to Epigrimyiini this tribe appeared as sister to the voriine clade (clade 7) that include the Camplylochetini and Wagneriini, forming the following hypothesis: (Eutheriini (Camplylochetini + Wagneriini)). Eutheriini is a highly autopomorphic tribe, i.e., wing with alula unusually long and darkened (74: 1), female terminalia with sternite 8 with deeply grooved with lightly sclerotized extension (171: 4) and egg with posterodorsal window (181: 2), but, historically, many authors do not found many shared traits to point for a reliable sister group hypothesis. Herein, however, we have found 9 shared apomorphic characters (see appendix 5) that places this tribe as sister to (Camplylochetini + Wagneriini). This hypothesis is very close to the one proposed by Verbeke (1962) that included Eutheriini as adjacent to his Voriinae (Dexiinae, in part).

4.5. The revival of Camplylochetini and Wagneriini

Camplylochetini and Wagneriini, as others voriines, were traditionally placed within Tachininae (Townsend, 1934-1942; Mesnil, 1939; Guimarães, 1971; Crosskey, 1976). After the works of Verbeke (1962) and Herting (1957), in addition to the consolidation of Tschorsnig (1985), these tribes began to be considered as Dexiinae by the putative synapomrphies of the male terminalia: platiform pregonite and the connection between the basiphallus and distiphallus hinged and angled. Hence, from Herting (1984) onwards (O'Hara & Wood, 2004;

Cerretti et al., 2014; Stireman et al. 2018; O'Hara et al., 2020) Camplylochetini, Wagneriini and the others voriines where considered within Dexiinae. Camplylochetini and Wagneriini however, were considered as very close to the voriines and their separate rank were dubiously maintained (Crosskey, 1976). Consequently, both tribes were considered as synonymous with Voriini (O'Hara et al., 2020).

Members of Camplylochetini (*Campylocheta*) and Wagneriini (*Periscepsia, Kyrbia* and *Wagneria*) were included by Stireman et al (2018), with Camplylochetini (*Campylocheta*) very close related to Wagneriini (*Periscepsia*) being nested in the same clade, in addition to the single genus *Myiotrixa* from the tribe Myiotrixini. The remaining genera of Wagneriini (*Kyrbia* and *Wagneria*) were recovered as a clade within the polyphyletic Voriini. Our phylogenetic hypothesis however, provided plenty evidence that both tribes deserves a tribal ranking, following their monophyly; Camplylochetini present some outstanding synapomorphies derived from the male terminalia as discussed by Verbeke (1962): phallopodeme with intermedium pad like with microtrichia (30: 2), distiphallus with acrophallus presenting globose expansion (141: 2) and pregonites fused, encircling phallapodem (146: 3), thus, following those remarkable synapomorphies, we propose to revalidate this tribe from the synonymy from Voriini. Similarly, Wagneriini was also recovered as monophyletic, although not as strongly and the former tribe, because it presents no autapomorphies excepted for the 15 homoplastic apomorphic traits. It is worth to mention that Wagneriini presents as homoplastic apomorphies some traits that are usually related to the Voriini: male terminalia with tergite 6 membranous (99: 2), male terminalia with sternite 6 superimpose at right with segment 7 (111: 1), surstylus with inner side carinate (118: 2) and distiphallus bare (143: 1). In conclusion, we have confirmed the polyphyletic nature of the voriines as found by Stireman et al (2018), but as we are, differently to Stireman et al (2018), proposing to revalidate Camplylochetini and Wagneriini (that confirmed the voriines polyphyly), we have further advanced the phylogenetic knowledge of the complex and difficult clade of the Voriini.

4.6. Epigrimyiini: sister group of Spathidexiini

Similarly to the Eutherini, the New World tribe Epigrimyiini (*Epigrimyia* Townsend and *Beskia* Brauer & Bergenstamm) was historically associated to the Phasiinae for parasitizing the Heteroptera (Guimarães, 1977), and this alone, was one of the main reason for being allocated with the phasiines (e.g., Guimarães, 1971; Herting, 1983). Verbeke (1962), however, was the first to note the affinities of Epigrimyiini (*Epigrimyia*) to the dexiines, mainly to his "Voriines" by the structures of the distiphallus. This vision was further confirmed by

Tschorsnig (1985) who placed *Beskia* and *Epigrimyia* in the Voriini of the Dexiinae, and by the phylogenetic analysis based on DNA by Blaschke et al. (2018) and Stireman et al. (2018) that this tribe belong to Dexiinae. Our morphological analysis of Dexiinae also confirm this placement within Dexiinae (Epigrimyiini were not represented in Cerretti et al., 2014), and this is the first morphological phylogenetic evidence of this placement. As already discussed, our results differ from the molecular evidence of Blaschke et al. (2018) and Stireman et al. (2018), with Eutheriini nested with the voriines and Epigrimyiini sister group with Spathidexiini (clade 10). This placement suggested herein is based on the synapomorphy of the female terminalia: sternite 8 spatulate (171:1) on ACCTRAN and first instar larva with undeveloped posterior spiracle (201: 2). Both traits are, probably, related to their oviposition strategy, and contrary to the molecular evidence, supports the close affinity with Spathidexiini. Epigrimyiini is highly supported tribe with the autapomorphy of wing with bent of M reaching wing margin at the same point (81:1), in addition to the 17 apomorphic character states.

4.7. A narrow Voriini and the revival of Spathidexiini

The voriines were always a very confuse and complex group that was placed sometimes in the subfamily Dexiinae, Tachininae and, even one of their own, Voriinae. More recently these groups were conclusively placed within Dexiinae by the molecular (Stireman et al. 2018) and morphological evidence (Cerretti et al., 2014). The internal resolution of the voriines is very controversial and some very disparate opinions appeared in the works of the some of the experts of the family; the most recent proposition (O'Hara et al., 2020) is of an enlargement of this tribe by putting in synonymy various tribes that were previously valid: Campylochetini, Thelairini, Wagneriini, Phyllomyini, Eriotrichini. However, no phylogenetic argumentation was developed by those authors that proposed this enlarged vision of the voriines (mainly Herting, 1984), making this classification open and disputed. When the phylogenetic evidence became available by both the works of Stireman et al. (2018) and Cerretti et al. (2014), the complexities of this group was confirmed, as Voriini was suggested as paraphyletic by the morphological evidence (Cerretti et al., 2014) and polyphyletic (e.g., *Eulasiona* appeared within Tachininae) by the molecular evidence (Stireman et al., 2018). Later, Stireman et al. (2018) suggested the possibility that many tribes may have to be erected or redefined if they are to reflect monophyletic groups. In the light of these discussion and aligned with our results, we further break the voriine clade to one more revalidated tribe, the Spathidexiini (*Spathidexia* Townsend, *Parodomyiops* Townsend, *Polygaster* Wulp, *Thelairodes* Wulp). Thompson (1963) already noted the great resemblance between those genera and proposed that they could be close phylogenetically. With 5 homoplastic apomorphic traits, including female terminalia with sternite 9 elongated, same length as the long and modified sternite 8 (176: 2) and first instar larva with antenna present and well developed (189: 0), this group is revalidated for the first time since its first conception made by Townsend (1912).

The Voriini *sensu lato*, as an enlarged tribe, is polyphyletic. Hence, in order to propose a monophyletic tribe, we have proposed the revalidation of Campylochetini **tribe rev**., Eriotrichini **tribe rev**., Phyllomyini **tribe rev**., Thelairini **tribe rev.**, Spathidexiini **tribe rev.** and Wagneriini **tribe rev.** as monophyletic groups, that removed the polyphyly of the Voriini *sensu lato*. Our Voriini *sensu stricto*, as newly delimited herein, is a monophyletic tribe with 69 genera (appendix 4). The traditional character states that were used to support the Voriini were recovered as apomorphic homoplasies for the taxa included in this tribe; for instance, the male terminalia with sternite 6 superimpose at right in relation to segment 7 (111: 1), surstylus with inner side carinate (118: 2) and distiphallus very elongate, ribbon-like (132: 1), all from Tschorsnig (1985). Thus, as it happened to the putative synapomorphies of Dexiinae, these traits did not result in synapomorphies for all the voriines and reappeared in some other clades as well (e.g., Wagneriini).

4.8. *Torocca* within Sophiini

Sophiini is a remarkable tribe with its members being easily recognized by presenting body, legs, wing and abdomen elongate and legs laterally compressed in female, in addition to some of its taxa (*Cordyligaster* Macquart) presenting a petiolate abdomen (Santis, 2018). The taxa included in this tribe was thought to be an artificial assemblage (Guimarães, 1982) as no putative synapomorphy was found for them. However, Santis (2018) discussed that the absence of abdominal sternites 2 to 4 (wholly membranous) could be a derived character for Sophiini and this trait was found to be an apomorphic homoplasy for this group (97: 1); also found in *Doleschalla* (Dexiini). Herein, our phylogenetic hypotheses suggest that Sophiini is a monophyletic group with its traditional assemblage of taxa (appendix 4) in addition to the inclusion of the genus *Torocca* Walker from the Oriental, Paleartic and Australasian regions. This hypothesis confirms partially the visions of Mesnil (1974) that assigned *Torocca* with *Cordyligaster* in a subgroup within his Doleschaliina (the other group includes *Doleschalla* only). Later, Mesnil (1974) further discussed that his group that contains *Torocca* and *Cordyligaster* are close to the Thelairini; this confirms the earlier views of Verbeke (1962) that included in his “Thelairines” (Thelairini, in part) a member of Sophiini (*Euanthoides* Townsend) based on the general form of the distiphallus. This configuration was further confirmed by our phylogenetic hypothesis, as the clade (13) (Sophiini (Philomyiini + Thelairini)); however, the characters supporting those tribes are not strong and this hypothesis is currently subject to further revision by the inclusion of more traits and taxa.

4.9. Phyllomyini + Thelairini

The sister group of Phyllomyini **rev. stat.** with Thelairini obtained herein is another confirmation of the visions of Mesnil (1974) and Verbeke (1962) that discussed the close relationship of these tribes. Furthermore, we provided evidence that Phyllomyini (*Engeddia* Kugler, *Leptothelaira* Mesnil & Shima, *Itamintho* Townsend, *Phyllomya* Robineau-Desvoidy) is a monophyletic tribe supported by 5 apomorphic homoplasies, including the female terminalia with sternite 8 spoon-like (171: 6) and first instar larva with antenna present and well developed (189: 0); differently to Mesnil (1974) that included in this tribe only the genus *Phyllomya*. On the other hand, we found support for the monophyly of Thelairini by excluding from it the genera *Spathidexia* Townsend, *Parodomyiops* Townsend, *Polygaster* Wulp, *Thelairodes* Wulp that composes our revalidated tribe Spathidexiini. When restricted by the genera traditionally placed in Thelairini (appendix 4), this tribe is recovered as monophyletic by 8 apomorphic homoplasies mainly from the distiphallus; i.e., distiphallus with extension of the dorsal sclerite less than half to the median ridge (133: 0), distiphallus with the extension of the dorsal sclerite equal sized along its extension (135: 0), distiphallus with ventral sclerite not fused to the dorsal sclerite (139: 1) and distiphallus with acrophallus as a granular structure (141: 1).

4.10. Telothyriini and Eriotrichini tribe rev.

The monophyly of the monogeneric Telothyriini was never disputed in the tachinid literature, as its members present their thoracic setae ramificated (48: 2), or plumose hairs (Thompson, 1963). This trait was found herein to be a synapomorphy for Telothyriini; furthermore, we found evidence of this tribe being close to Eriotrichini, Uramyini and Dexiini - clade 16 (Telothyriini (Eriotrichini (Uramyini + Dexiini))). *Telothyria* and *Eriothrix* were recovered as sister group together with a clade of Dufouriini and other voriines by Stireman et al., (2018); thus, the proximity of those genera is further confirmed by the molecular evidence. On the other hand, Eriotrichini, as proposed by Mesnil (1974), was put in synonymy with Voriini since the work of Herting (1984) and was maintained by subsequent authors (Tschorsnig, 1985; O’Hara & Wood, 2004; O’Hara et al., 2020). However, as argued, the Voriini *sensu lato* was recovered as polyphyletic (same result as Stireman et al., 2018), with the members of Eriotrichini being closer to the Dexiini - clade 17 (Eriotrichini (Uramyini + Dexiini))) - than to the Voriini. Thereby, we propose to revalidate this tribe for the following genera: *Dexiomimops* Townsend, *Eriothrix* Meigen and *Feriola* Mesnil. This phylogenetic hypothesis is very similar to the views of Mesnil (1974), as he put the taxa of our concept of Eriotrichini as very close related, i.e., his combined group of Eriotrichina and Dexiomimopsina.

4.11. The sister group of Dexiini and an enlarged Uramyini

The Uramyini was, before our results, a New World tribe that are one the more typical tachinid groups by presenting the eyes are thickly pilose and some members presenting its males with a conical tail on the last abdominal segment (Guimarães, 1980). Herein, our phylogenetic hypothesis suggests that Uramyini must be enlarged to include the genera: *Blepharomyia* Brauer & Bergenstamm, *Dischotrichia* Cortés, *Eulasiona* Townsend, *Metopomuscopteryx* Townsend, *Muscopteryx* Townsend, *Prosopochaeta* Macquart, *Piriona* Aldrich, *Trafoia* Brauer & Bergenstamm and *Trichodischia* Bigot; in addition to the formerly typical members of this tribe (appendix 4). This clade (18) presents 4 apomorphic homoplasies, being two of them from the first instar larva: cephaloskeleton presenting the sclerite of the salivary gland subsquared (206: 5) and the intermediate region with median enlargement (210: 0). The configuration of this newly delimited Uramyini is somewhat recovered by the molecular evidence by Stireman et al. (2018), as this tribe (represented by *Thelairaporia* and *Uramya*) showed a close relationship to the genera *Micronychiops*, *Trafoia*, *Metopomuscopteryx* and *Muscopteryx*; with the exception of *Micronychiops*, all those genera are included in our enlarged Uramyini. Worth of noticing is that *Thelairaporia* and *Uramya*, as representatives of Uramyini, were recovered herein as a monophyletic group by two synapomorphies: abdominal sternites 1 and 2 visible (96: 2) and sternite 5 with *sensila trichodea* on base (105: 1). Furthermore, the present configuration of the taxa in this tribe is, once again, somewhat close to the ideas expressed by Mesnil (1974); he believed that the Uramyini and the genus *Trichodischia* would belong to his Eriothrixina and that Eulasionina, with its only genus *Eulasiona (Paramuscopteryx* Townsend is a subgenus of *Eulasiona* for Mesnil, 1974), would be very close to Eriothrixina (mainly by the genus *Blepharomyia*). Our phylogenetic hypothesis of *Eulasiona* within Dexiinae is new for the tachinid phylogeny, as Stireman et al. (2018) recovered this genus within Tachininae. Finally, and rather surprisingly, we found that Uramyini is sister group to Dexiini by the synapomorphy of the first instar larva (segment V with dorsal microtrichia (194: 2)), and we think that additional research is needed to confirm this phylogenetic hypothesis.

4.12. A new hypothesis and classification for Dexiini

Dexiini with 140 genera, is the largest tribe of Dexiinae and the one that imposes difficult challenges in relation to its taxonomy and, mainly, its phylogeny. The Neotropical taxa of Dexiini, for instance, is in a desperate need of a thoroughly revision of its genera and former tribes mainly because of the poor information about the male and female postabdomen and immature stages, in addition to the large proportion of adult material that remains undescribed aligned with the difficult to identify the ones already described, still relying on comparisons with the type material. Zellini, as an example, is currently considered as synonymous with Dexiini and presented 10 genera, that after some taxonomic revisions, decreased to 7 as *Opsozelia* Townsend showed to be indistinct from *Zelia* Robineau-Desvoidy (Dios & Santis, 2019) and *Tromodesiopsis* Townsend from *Ophirodexia* Townsend (Santis, accepted) and, finally, *Tromodesiana* Townsend was considered as *insertae sedis* in Tachinidae (O'Hara et al., 2020). In addition, it is very possible that most of the 7 remaining genera from the former Zeliini became indistinct from *Zelia* as well.

The phylogenetic hypothesis recovered by the present phylogeny shows some considerable differences from the current configuration of Dexiini: (1) the following two tribes, that were valid before this work, and are considered as synonymous with Dexiini: Doleschaliini and Rutiliini and (2) the inclusion of *Stomina* and *Subfischeria* (Stominini) and *Rhamphina* (Rhamphinini) within Dexiini, former in the Voriini *sensu lato* – a proposition already pointed by Verbeke (1962). The configuration of *Stomina* as sister to *Rhamphina* and the remaining Dexiini is something already hypothesized by Cerretti et al. (2014); the clade K (*Stomina* + Dexiini) of Cerretti et al. (2014) is almost the same as recovered herein (only with the addition of *Rhamphina* as sister to all other Dexiini) and confirms this configuration. Hence, by delimitating Dexiini broad enough to include both *Stomina* and *Rhamphina*, six apomorphic homoplasies are proposed for this tribe, including the following: male terminalia with distiphallus equal sized along its extension to the dorsal sclerite (135: 0); first instar larva with small and irregular plates dermal cuticle (182: 2); segment XII with sensorial stylus (199: 1) and posterior spiracle with felt chambers in a tubular process (203: 2). The presence of the first instar larva with small and irregular plates dermal cuticle (182: 2) is one of the traditional putative synapomorphies of Dexiini (Thompson, 1963), that reflects the evolutionary adaption of their active first-instar larva, deposited freely on soil, rotting wood, etc., in which they use those spine dermal plates to search out their hosts. The other traditional synapomorphies of Dexiini, mainly related to the male terminalia, are present in the clade (21) that contains all

Dexiini except *Stomina* and *Rhamphina*, and it presents 10 apomorphic homoplasies, including: frontal setae ending before the base of antennae insertion (9: 1); parafacial bigger, more than 2X the width in relation to postpedicelum (20: 1); and, from Tschorsnig (1985), male terminalia with surstylus broad, massive (116: 0); distiphallus with acrophallus as a granular structure (141: 1); pregonite platiform, with strong sclerotization anteriorly (150: 0) and pregonite platiform and strong downward directed (151: 1). Cerretti et al (2014), for instance, obtained for Dexiini two trait from those obtained for our clade 21: male terminalia with surstylus broad, massive (116: 0); distiphallus with acrophallus as a granular structure (141: 1). Stireman et al. (2018), on other hand, obtained a polyphyletic Dexiini, with *Microchaetina* in Tachininae (same result recovered herein); in addition, they supported the hypothesis of the Australasian and Oriental Rutiliini being nested within Dexiini.

Rutiliini within dexiines

The Rutiliini (appendix 4) composes an extremely beautiful group, often very sizeable robust flies which frequently display brilliant metallic colors and conspicuous patterns (Crosskey, 1973). Although in his revision of the Rutiliini Crosskey (1973) discussed the problem of presenting a trait that is common to all members of this tribe (a putative synapomorphy), this tribe was always considered as valid and distinct from Dexiini. However, Verbeke (1962) and Tschorsnig (1985), based on traits from the male terminalia, could not distinguished the Rutiliini taxa from the dexiines, thus they have included it within Dexiini. Similarly, the molecular evidence proposed by Stireman et al. (2018) and our morphological phylogenetic evidence suggests the placement of Rutiliini nested within Dexiini; thus, herein Rutiliini is nested well within Dexiini being sister group of the Australasian taxa *Rutilotrixa* and *Senostoma*; *Rutilotrixa*, furthermore, is considered to present some extent reminiscent to *Chetogaster*, a genus doubtfully placed in the Rutiliini (Barraclough, 1992). The former Rutiliini is supported by one synapomorphy, first instar larva with long spine-like microtrichia ventrally (192: 1), in addition to six apormorphic homoplasies, including the first instar larva with small irregular plates (182: 2), polygonal cuticular plates (186: 1), cuticular plates only on anterior portion (187: 1) and cephaloskeleton with mouth hook large, quadrate (207: 3); thus, this assemblage is supported mostly by the traits from the larva. The putative synapomorphies that has been historically associated to Rutiliini (Crosskey, 1973) where, instead, supportive to the clade (*Prodiaphania* (*Formosia* + *Rutilia*)) - scutum with postalar callus with supernumerary setae (53: 1) and scutellum with supernumerary setae (58: 3) - in addition to the scutum forming a transverse row of strong setae in the hindmost part between acrostichal and dorsocentral setae (53: 0) being a synapomorphy for *Formosia* + *Rutilia*. Although these clades, i.e., *Formosia* + *Rutilia*, are strongly supported, Rutiliini is suggest to be synonymous with Dexiini as most putative synapomorphies were not recovered for the tribe and their taxa were recovered well within Dexiini (same result obtained by Stireman et al. 2018).

Doleschaliini: a former monotypic tribe of Dexiinae

This monotypic tribe (*Doleschalla* Walker) includes one of the most slender-bodied and elongate-legged Tachinidae (Crosskey, 1976) that are distributed along the Oriental and Australasian regions. Stireman et al. (2018) recovered Doleschallini well nested within Dexiini, similarly to Rutiliini, and as sister group of *Zelia* and to a clade that includes *Dexia* and *Trixodes*. The genus *Doleschalla*, as discussed by Crosskey (1976) and Barraclough (1992), would be a monophyletic group, and the three autapomorphies recovered herein confirms it: ocellar triangle with 2 ocellus (4: 2), fronto-orbital plate about ½ the head length in profile (11: 2) and abdominal tergites subparallel-sided (89: 1), in addition to 11 apomorphic homoplasies. However, their rank as tribe could not maintained as they showed to be nested within the dexiines and, in addition, showed many shared traits with them. Differently to Stireman et al. (2018), our morphological evidence recovered *Doleschalla* sister group to all remaining Dexiini and not close do *Zelia* and *Dexia*.

Former invalid groups and tribes in Dexiini

Crosskey (1973) was one of the first authors to propose that some tribes of Townsend in his *Manual of Myiology* (1934-1942) would not be distinct from Dexiini; those tribes were the Dexillini, Theresiini, Trichodurini, Trixodini, Prosenini and Zeliini. This view was incorporated by O’Hara & Wood (2004) and O’Hara et al. (2020) and confirmed by the phylogenetic hypothesis of Stireman et al. (2018). Our phylogenetic hypothesis gives even further confirmation that those tribes of Townsend are not natural, i.e., nonmonophyletic, and are best considered as synonymous to Dexiini. Zeliini is one of these former tribes; although forming a clade (23) based on three apomorphic homoplasies, katepisternum with 2 setae (64: 2), abdominal setae different disposition different disposition (93: 1) and male terminalia with pregonite fused with seam to postgonite (144: 1), clearly they do not constitute a group that differ enough from the other dexiines to rank them as a separate tribe.

4.13. Genera excluded from Dexiinae

The genera *Microchaetina*, *Pseudodexia* and *Polygastroptery* could not be placed in Dexiinae or any of the higher-level group (like Dufouriinae) with certainty. These genera does not present the male terminalia with connection between basiphallus (dorsal sclerite) and distiphallus membranous (125: 0), a trait herein hypothesized as a synapomorphy of (Dexiinae (Phasiinae + Dufouriinae)), or the important trait of male terminalia with membranous connection between basiphallus (dorsal sclerite) and distiphallus with 180º movement capacity (126: 1); accordingly, these genera are removed from Dexiinae, and *Microchaetina* and *Pseudodexia* are *incertae sedis* in Tachininae. *Pseudodexia* has a history of doubtful placement between the Blondeliini (Exoristinae) and Dexiinae. Wood (1985) in his revisionary work of the blondellines, placed *Pseudodexia* within this tribe; later, however, he and Zumbado (Wood & Zumbado, 2010) wrote that this earlier placement was an error because the male terminalia would indicate a placement in the Dexiinae. Herein, we were able to dissect the male terminalia and could conclusively determine that *Pseudodexia* does not present the typical trait of the male terminalia of Dexiinae (mainly the basiphallus and the distiphallus present a sclerotized connection, and the pregonites are not platform); thus being one of the reasons for its phylogenetic placement outside Dexiinae. *Polygastroptery* never had its male and female terminalia or immature stages investigated before the present study; thus, by dissecting one species of this genus, we could confirm that, as *Microchaetina* and *Pseudodexia*, it presents the trait of the basiphallus and distiphallus with a sclerotized connection. Surprisingly, we could find some macrotype eggs by dissecting the female abdomen, and this was one of the reasons for being placed as sister group of the phasiines. However, at the moment, until further studies become available, we think it is prudent to regard this genus as *incertae sedis* in Tachinidae.

Opsophagus Aldrich, 1926 **stat. rev.**

Opsophagus Aldrich was erected for the inclusion of two species, *O. nigripalpis* Aldrich, 1926 and *O. ornatus* Aldrich, 1926, from Peru, and had one more species included from Chile, *O. cortesi* Caltagirone, 1966. This poorly known genus was not further studied or had any detailed or comparative studies performed. Wood & Zumbado (2010) hinted the possibility of this genus being synonymous to *Cyrtophleba* Rondani, and this hypothesis was confirmed by O'Hara et al (2020) by formally putting *Opsophagus* as synonymous to *Cyrtophleba*. The present phylogenetic study, however, does not support this synonymy: herein *Opsophagus* is sister group to *Ateloglutus* and *Cyrtophleba* is basal to the Voriini *sensu stricto*, being sister to *Paedarium*. Thereby, our hypothesis does not support the views of O'Hara et al (2020) and we revalidate this genus from the synonymy with *Cyrtophleba*, thereby: *Opsophagus* Aldrich, 1926 **stat. rev.**; *Opsophagus nigripalpis* Aldrich, 1926 **comb. nov.**; *Opsophagus cortesi* Caltagirone, 1966 **comb. nov.**; *Opsophagus ornatus* Aldrich, 1926 **comb. nov.**

5. Conclusions

Phylogenetic trees are used as resumes of many evolutionary events (effects), and the lack of phylogenetic knowledge of the evolutionary patterns is often a major restraint on inference of evolutionary process. Once those patterns are recognized, we can pursue the evolutionary causes for these patterns by searching for the mechanisms (e.g., genetical, embryological), functions and every significant biological evidence, to support which process better explain for the evolution of a particular trait.

In the light of the above discussion, this study represents the most comprehensive phylogeny of Dexiinae to date, based on 213 morphological characters, and provides the first hypothesis underpinning our understanding of the evolutionary relationships in the group. Those morphological characters of adults along with male terminalia are traditionally used as main character sources in Tachinidae systematics, and this study demonstrated that characters from eggs, larvae, female terminalia and spermatheca have great systematic importance, as they mutually supported clades and resulted in important synapomorphies for several taxonomic levels. One of the outstanding results of our study is the confirmation of the initial view of Verbeke (1962), later followed by Crosskey (1976; 1980), Cantrell (1988) and Barraclough (1992), that Dufouriini do not belong to Dexiinae nor Phasiinae. In addition, according to the results obtained herein, the following tribes are removed from Dexiinae: Oestrophasiini, Freraeini and Dufouriini, constituting now their own subfamily, Dufouriinae **rev. stat.** being a sister group of Phasiinae. The Voriini *sensu lato* as previously proposed (O'Hara et al., 2020) is polyphyletic, and in order to propose this tribe as monophyletic, we revalidated Campylochetini **tribe rev**., Eriotrichini **tribe rev.,** Phyllomyini **tribe rev**., Thelairini **tribe rev.,** Spathidexiini **tribe rev.** and Wagneriini **tribe rev**.; and the Voriini *sensu stricto*, as herein defined, is composed by 69 genera. Eutherini and Epigrimyiini, taxa historically with a doubtful classification, are confirmed as dexiines. Finally, Doleschaliini and

Rutiliini are nested within Dexiini and are, following this phylogenetic hypothesis, put in synonymy with Dexiini (see appendix 4).

Phylogenies are complex historical hypotheses, and each node correspond to a unique character state transformation connecting a set of terminal taxa. In this sense, we tried to include the most complete source of data to infer the phylogeny of Dexiinae in the most comprehensive way possible, thus this phylogenetic hypothesis follows the principle of total evidence (Kluge, 1989; Salmon, 1998). We followed this methodological principle to avoid, in the most comprehensive way, some problems that phylogenetic hypothesis may present; it may be negatively affected by issues of homology, homoplasy, coding and taxon or character sampling. Even so, the present hypothesis can be viewed as an improved hypothesis in relation to previous classification systems of the subfamily, due to the use of the largest dataset so far, in a phylogenetic analysis, and for the first time included all the valid and invalid tribes of Dexiinae. Finally, it is hoped that the present phylogenetic analysis of Dexiinae will be of value for future studies dealing with evolutionary processes and will provide a tool for applied sciences like the field of biological control.

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Appendix 1. List of characters used in the phylogenetic analysis.

List of characters

ADULT

Head

1. Eyes, separation, holoptic males with dicoptic females (L=11; CI=9; RI=72): (0) absent; (1) present.

2. Eye, on apical ¼ going to occiput (L=1; non-informative): (0) not reaching occiput; (1) going to occiput (Fig. 4A).

3. Eye, surface (L=10; CI=10; RI=52): (0) bare; (1) with setulae.

4. Ocellar triangle, number of ocellus (L=1; CI=100; RI=100): (0) 3; (1) 2.

5. Ocellar setae, inclination, in females (L=12; CI=25; RI=55): (0) proclinate; (1) lateroclinate; (2) reclinate; (3) reduced to setula.

6. Postocellar seta (L=7; CI=14; RI=64): (0) absent; (1) present.

7. Vertex, inner vertical setae, in females (L=7; CI=14; RI=40): (0) absent; (1) present.

8. Ocellar triangle, adjacent prionosity, in relation to frontal vittae (L=7; CI=14; RI=71): (0) ending before; (1) going after.

9. Frontal setae, presence in relation to the base of antennae insertion (L=9; CI=11; RI=88): (0) beyond; (1) before (Fig. 4C).

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for Phasiinae + Dexiinae with reversion to state 0 for *Leucostoma*. While in DELTRAN state 1 is an apomorphic homoplasy in *Imitomyia*, *Phasia* + *Eutrichopoda*, *Microsoma* + *Freraea* (Freraeini) and *Chetoptilia* + *Dufouria* (Dufouriini).

The character state 1 was, since its first conception (Mesnil, 1939), considered as very relevant for the delimitation of Dexiinae. Although the majority of the Dexiini herein included presents this trait, it is considered as homoplastic, reappearing in various taxa outside Dexiinae, e.g., *Cholomyia* (Tachininae) and some phasiines (e.g., *Phasia* and *Eutrichopoda*). In addition, the same lack of phylogenetic signal for this character state was found in Cerretti *et al*. (2014) for Dexiinae.

10. Fronto-orbital plate, in relation to the antennal axis (in profile) (L=22; CI=4; RI=66): (0) not elevated; (1) elevated.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for Phyllomyiini + Thelairini with reversion to state 0 for *Xanthodexia*, *Allothelaira* and *Thelaira*. While in DELTRAN state 1 is an apomorphic homoplasy in Phyllomyiini and in *Halydaya*.

11. Fronto-orbital plate, degree of elevation in profile from the antennal axis (L=1; CI=100; RI=100): (0) less than ½ the head length; (1) about ½ the head length.

12. Fronto-orbital plate, frontal setae, in males (L=19; CI=5; RI=58): (0) just with setae; (1) with setae and setulae (Fig. 4B).

13. Fronto-orbital plate, setae alongside the frontal setae (L=4; CI=50; RI=0): (0) just one row; (1) three to four rows of setae; (2) two rows.

14. Fronto-orbital plate, orbital setae, in males (L=11; CI=9; RI=70): (0) absent; (1) present.

15. Fronto-orbital plate, orbital setae, number o proclinate setae, in males (L=5; CI=60; RI=83): (0) 2; (1) 3; (2) 5; (3) 7.

16. Fronto-orbital plate, proclinate orbital setae, in females (L=23; CI=21; RI=48): (0) 2; (1) forming a row of several setae; (2) 3; (3) 1; (4) 5; (5) absent.

17. Fronto-orbital plate, orbital setae, females (L=13; CI=23; RI=54): (0) 2 proclinate; (1) 3 proclinate; (2) 1 proclinate; (3) 5 proclinate; (4) 7 proclinate.

18. Frontal vitta, visibility on upper third, in males (L=11; CI=9; RI=33): (0) visible; (1) invisible.

Ambiguous character, however ACCTRAN or DELTRAN optimization are shown to be equal in this clade, that is, state 1 is an apomorphic homoplastic for *Cholomyia*.

19. Frontal vitta, interfrontal setae (L=14; CI=7; RI=56): (0) absent; (1) present.

20. Parafacial, width in relation to post pedicelum (in obliquely view) (L=24; CI=12; RI=70): (0) smaller, less than 1X; (1) about the same 1X to 1.5X; (2) bigger, more than 2X (Fig. 4E); (3) 5X (Fig. 4F).

21. Parafacial, surface (L=23; CI=8; RI=48): (0) bare (Fig. 4D); (1) setula; (2) seta (Fig. 4B).

22. Parafacial, disposition of setae (L=4; CI=75; RI=50): (0) varios, as a row (doward directed); (1) only 1 (doward directed); (2) 1 (upward directed); (3) scattered.

23. Face, lunule, surface (L=1; CI=100; RI=100): (0) bare; (1) setula.

24. Frontoclypeal membrane, in relation to the lower facial margin (L=3; CI=33; RI=0): (0) in the same level; (1) well above.

25. Face (L=14; CI=14; RI=75): (0) without elevation; (1) mid-facial elevation (Fig. 4E); (2) facial carina (Fig. 4D).

According to Barraclough (1992), a facial carina differs from a mid-facial elevation by extending between the antennal bases to the epistomal region.

The history of the presence of a facial carina to circumscribe Dexiinae is very old, being first ascribed for Macquart (1844) for his Dexiairiae (Dexiinae, in part). Likewise, Brauer and Bergenstamm (1889–1895), Mesnil (1939; 1980) and Thompson (1963) included this trait to delimitate Dexiinae. In the present analysis however, this character state is not a synapomorphy of Dexiini nor Dexiinae; the presence of a facial carina is found scattered along various taxa in the phylogenetic tree (Fig. 3) and does not constitute a synapomorphy for any of the tribes studied. Furthermore, in Cerretti et al (2014) the presence of a facial carina (30:1 of Cerretti *et al*. 2014) was an apomorphic homoplasy for their clade K (*Stomina* (*Billaea* (*Dexia* + *Prosena*) (*Zeuxia* (*Estheria* + *Trixa*), thus not as informative as the earlier authors hypothetized.

26. Face, frontal vittae width in relation to antena insertion (L=1; non-informative): (0) broad; (1) narrow.

The state 1 is autapomorphic for *Neozelia*.

27. Shape of facial ridge (in lateral view) (L=9; CI=11; RI=61): (0) evenly concave; (1) convex.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for Uramyini + Dexiini with reversion to state 0 for *Uramyia* + *Thelaroporia* and (*Pelycops* (*Dasyuromyia* (*Morphodexia* +*Psecacera*). While in DELTRAN state 1 is an apomorphic homoplasy in Telotyriini, Eriotrichini, *Trafoia*, *Uramyia* + *Thelaroporia* and (*Pelycops* (*Dasyuromyia* (*Morphodexia* +*Psecacera*).

28. Face, frontal vittae width in relation to antena insertion (L=9; CI=11; RI=61): (0) absent; (1) present.

29. Face, lower facial margin (L=19; CI=5; RI=60): (0) prominent; (1) not prominent.

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for Dexiini While in DELTRAN state 1 is an apomorphic homoplasy in *Rhamphina* and *Stomina*.

30. Pedicel, seta, length of adjacent setae (L=11; CI=27; RI=63): (0) all about same size; (1) one longer, about three times longer; (2) two strong; (3) various setae, equally longer.

31. Antenna, scape, form (L=1; CI=9; RI=80): (0) raised (forward) (Fig. 4A); (1) not raised (same aligned with face).

32. Postpedicel, width, sexual dimorphism (L=19 CI=100; RI=100): (0) males with twice the width of females; (1) male equal width with females.

33. Antenna, arista, setulosity (L=15; CI=13; RI=81): (0) pubescent (Fig.4A); (1) micropubescent; (2) plumose (Fig. 4C).

The presence of a plumose arista (33: 2) is another historicaly revelant trait for Dexiinae. Macquart (1844) included this trait to delimitate his Dexiairiae (Dexiinae, in part) and even if Mesnil (1939; 1980), a centruey later, proposed that this trait was only often present in this subfamily. This character state showed to be present in almost all Dexiini included herein; only absent in the Chilean dexiines (*Pelycops* (*Dasyuromyia* (*Morphodexia* +*Psecacera*) and *Stomina*, *Heterometopia Rutilotrixa* and *Trixa*. However, as expected, this trait lacked a phylogenetic signal for Dexiinae (equally to Cerretti *et al*., 2014) and it is also present in some outgroups, e.g., *Calliphora* (Calliphoridae) and *Cholomyia* (Tachininae).

34. Arista, width in relation to post pedicelum, in frontal view (L=2; CI=50; RI=94): (0) same; (1) enlargerd, larger.

35. Pedicel, length in relation to scape (L=4; CI=50; RI=90): (0) about 2X; (1) about 3X; (2) about 5X.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for (((Eutheriini (Wagneriini + Campylochaetini)) + (Voriini (Epigrimyini + Sphatidexiini))). While in DELTRAN state 1 is an apomorphic homoplasy in Eutheriini, Wagneriini and Voriini.

36. Gena, relative to the width of the combined length of the scape and pedicel (L=14; CI=7; RI=78): (0) greater (Fig. 4C); (1) less (Fig. 4B).

37. Genal dilation (L=3; CI=3; RI=97): (0) present, well developed (at least half as high as genal height) (Fig. 4C); (1) absent (Fig. 4B).

38. Vibrissa, degree of differentiation from supravibrissals (L=4; CI=25; RI=25): (0) differentiated; (1) undifferentiated.

39. Vibrissa, insertion in relation to lower facial margim (L=17; CI=11; RI=74): (0) in the same level; (1) above; (2) below.

40. Facial ridge, region of insertion of the vibrissae, surface (L=7; CI=28; RI=37):

(0) setulae, but only at the base (Fig. 4A); (1) setulae, but all the facial ridge; (2) bare.

41. Facial ridge, length of the setulae (at least one) above vibrissae insertion (L=9; CI=1; RI=55): (0) shorter, about ⅒ of vibrissae length; (1) longer, about ½ of vibrissae length.

42. Face, frontogenal suture in relation to the facial ridge in its broadest location (L=4; CI=25; RI=40): (0) narrow; (1) broad.

43. Palpus (L=1; non-informative): (0) present, with visible structures; (1) absent, invisible delimitations of structures (Fig. 4A).

44. Palpus, development, in relation to labellum (L=3; CI=33; RI=0): (0) minute, shorter; (1) about as long or longer.

45. Palpus, length in relation to scape and pedicelum together (L=6; CI=16; RI=16): (0) longer; (1) shorter.

46. Palpus, apical portion, setulae, in females (L=4; CI=25; RI=57): (0) absent; (1) present.

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for Sphatidexiini with a reversion to state 1 in *Parodomyiops*. While in DELTRAN state 0 is an apomorphic homoplasy in (*Polygaster* + *Spathidexia*) and *Thelairodes*.

47. Proboscis, prementum, length relative to the head (L=20; CI=10; RI=71):

(0) less than 0.5X; (1) 1x to 0.5 x; (2) 2x.

Thorax

48. Seta, shape (L=3; CI=66; RI=50): (0) thin and longer; (1) robust and shorter; (2) ramificated (Fig. 5A).

49. Prosternum, surface (L=3; CI=1033 RI=50): (0) setulouse; (1) bare.

50. Propleuron, surface (L=9; CI=11; RI=74): (0) bare; (1) haired.

51. Position of postpronotal setae, if three or more (Cerretti *et. al*., 2014) (L=6; CI=16; RI=76): (0) mid-basal seta in line, or nearly so, with inner and outer basal setae (i.e., three basal setae arranged in line); (1) mid-basal seta displaced anteriorly, forming a triangle with inner and outer basal setae.

Mesnil (1974) considered the character state 1 (figure 63 of Mesnil 1974) as delimitating Campylochetini. Although present in the Campylochetini included herein (*Campylocheta* + *Parahypochaeta*), this trait was also present as an apomorphic homoplasy in *Periscepsia*, most of Voriini, Thelotyriini and *Prosochaeta*; thus supporting (as an apomorphic homoplasy) the Mensil (1974) concept of Campylochetini. The same carater state (44:1 of Cerretti et al 2014) was coded as polymorphic in *Campylocheta* by Cerretti *et al* (2014) and was not recoverd as apomorphous for any voriine clade.

52. Scutum, postsutural region, hindmost part between acrostichal and dorsocentral setae (L=1; CI=100; RI=100): (0) forming a transverse row of strong setae (Fig. 5B); (1) just with setulae.

This trait was taken from the observations of Crosskey (1973a). Synapomorphy of *Formosia* + *Rutilia*.

53. Scutum, postalar callus, number of setae (L=1; CI=100; RI=100): (0) 2 to 3 (Fig. 5B); (1) supernumerary (5 or more).

This trait was taken from the observations of Crosskey (1973a). Synapomorphy of (*Prodiaphania* (*Formosia* + *Rutilia*)).

54. Supra-alar setae (L=2; CI=50; RI=75): (0) 2 to 4; (1) 0 to 1.

55. Suprasquamal ridge, surface (L=2; CI=50; RI=66): (0) bare; (1) haired (Fig. 5C).

This trait was taken from the observations of Crosskey (1973a).

56. Postalar wall, surface (L=1; CI=100; RI=100): (0) bare; (1) haired.

This trait was taken from the observations of Crosskey (1973a).

57. Scutellum, shape (L=8; CI=12; RI=77): (0) rounded (Fig. 5A); (1) triangular; (2) flattened (Fig. 5B); (3) convex.

58. Scutellum, chaetotaxy (L=6; CI=50; RI=88): (0) only with the regular setae, i.e., basal, lateral, subapical, apical and discal setae (Fig. 5A); (1) besides regular setae, with various erected setae in entirely surface; (2) besides regular setae, with various non erected setae in entirely surface; (3) 3 supernumerary (10 to 12).

59. Scutellum, subapical region (L=10; CI=10; RI=74): (0) with subapical seta; (1) just with setulae.

60. Scutelum, lateral region (L=17; CI=5; RI=55): (0) with lateral seta; (1) just with setulae.

61. Scutellum, central region (L=12; CI=8; RI=59): (0) with discal seta; (1) just with setulae.

62. Subscutellum, form (L=5; CI=40; RI=25): (0) not or very slightly convex (Fig. 5D); (1) strongly convex; (2) undeveloped.

63. Anterior spiracle, disposition of hairs (L=9; CI=11; RI=65): (0) slit closed by fringes of hairs; (1) slit not closed by fringes of hairs.

64. Katepisternum, number of setae (L=33; CI=12; RI=67): (0) 4 (1 posterior, 1 anterior and 2 median); (1) 3 (in position 1+1+1); (2) 2 (in position 1+1); (3) 1 (posterior seta); (4) 0.

65. Anepimeron, setae, degree of development (L=26; CI=15; RI=71): (0) at least one strong and long; (1) various equally strong but not longer than adjacent setae; (2) slim and short; (3) 2 strong; (4) undeveloped.

66. Anepimeron, length of the strong seta in relation to adjacent setulae (L=2; CI=50; RI=87): (0) 2 to 3 times; (1) 6 to 7 times.

67. Posterior spiracle, arrangement of the fringes (L=9; CI=11; RI=75): (0) mainly from the posterior region; (1) equally distributed on both sides.

68. Femur III, tarsu (L=1; non-informative): (0) only black setulae; (1) with golden setulae.

The state 1 is autapomorphic for *Pelycops*.

69. Fore coxae, anterior face (L=9; CI=11; RI=75): (0) with 6 or more setae; (1) 1 seta; (2) bare.

70. Postmetacoxal area (L=3; CI=33; RI=66): (0) membranous; (1) sclerotized.

Wing

71. Lower calypter, shape (L=3; CI=66; RI=66): (0) rounded lobes (Fig. 6C); (1) reduced to mere rounded rims (Fig. 6B); (2) tongue shaped.

72. Lower calypter, color (L=15; CI=26; RI=47): (0) hyaline; (1) smoky; (2) yellow; (3) white; (4) black.

73. Costal base, form (L=2; CI=50; RI=0): (0) as a regular narrowed structure; (1) explanate (Fig. 6D).

This trait was taken from the observations of Crosskey (1973a).

74. Alula, form (L=1; CI=100; RI=100): (0) short and concolor with the rest of wing; (1) unusually long and darkened (in contrast with the rest of wing) (Fig. 6A).

The state 1 is autapomorphic for *Euthera*.

75. Second costal sector, surface (L=4; CI=25; RI=72): (0) bare; (1) haired (ventrally).

76. Seta at base of vein R4+5, width in relation to the adjacent setae, dorsally (L=7; CI=14 RI=33): (0) large, twice the size; (1) short, about the same size.

77. Rs node, ventrally, surface (L=3; CI=33; RI=33): (0) bare; (1) setulose.

78. R4+5 vein, dorsally, setulosity (L=19; CI=15; RI=63): (0) only in the Rs node; (1) beyond the Rs node but before r-m; (2) beyond r-m; (3) bare.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for (((Eutheriini (Wagneriini + Campylochaetini)) + (Voriini (Epigrimyini + Sphatidexiini))). While in DELTRAN state 1 is an apomorphic homoplasy in Sphatidexiini and *Beskia*.

79. Vein R_1, surface (L=11; CI=9; RI=47): (0) bare; (1) setulose.

80. CuA_1, surface (L=4; CI=25; RI=25): (0) bare; (1) setulose.

81. Bent of M, angle (L=12; CI=25; RI=52): (0) vein reaches wing margin separately; (1) vein reaches wing margin at the same point; (2) forming a small petiole (as long as r-m) with R4+5 reaching wing margin at wing tip; (3) forming a long petiole (longer than r-m) R4+5 reaching wing margin at wing tip.

Ambiguous character. In ACCTRAN state 3 is an apomorphic homoplasy for ((Eutheriini (Wagneriini + Campylochaetini)). While in DELTRAN state 3 is an apomorphic homoplasy in Eutheriini and Wagneriini.

82. Length of the apical part of vein M between crossveins M and dm-cu (discal medial-cubital) (relative to section between dm-cu and bend of M) (Cerretti *et. al*., 2014) (L=3; CI=33; RI=88): (0) exceptionally oblique (Fig. 6C); (1) about equal in length (Fig. 6A).

Mesnil (1939; 1974) characterized the tribe Voriini with, among other traits, the very conspicuous nature of the state 0. This trait, however, was not recovered as synapomorphic for Voriini, instead, it appeared as an apomorphic homoplasy present in *Periscepsia* (Wagneriini) and in Voriini (except *Arrhinactia*). Cerretti *et al*. (2014), on other hand, recovered their Palearctic Voriini with this character state as synapomorphic (76:1 of Cerretti *et al*., 2014).

83. Vein rm, form (L=3; CI=33; RI=80): (0) straith; (1) sinuouse.

84. Radial-medial crossvein, form (L=2; CI=50; RI=66): (0) retracted, obviously closer to small crossvein than to cubitulus; (1) far out on disk of wing, nearer to cubitulus (bend of vein 4) than to small crossvein.

85. Discal medial crossvein, form (L=3; CI=33; RI=81): (0) straight; (1) sinuouse (Fig. 6D).

Abdomen

86. Dorsal connection between abdominal tergites (L=3; CI=33; RI=0): (0) not fused; (1) fused.

87. Chaetotaxy, form (L=3; CI=33; RI=33): (0) setae and setulae (Fig. 7B); (1) just setulae.

88. Seta, form (L=2; CI=50; RI=75): (0) setiform; (1) spine-like (Fig. 7A).

89. Tergites, length in relation to each other (L=1; CI=100; RI=100): (0) intermediate segments bigger than T1+2 and T5; (1) subparallel-sided, i.e, intermediate segments narrower than T1+2 and T5.

This trait was taken from the observations of Barraclough (1992). The state 1 is autapomorphic for *Doleschalla*.

90. Abdomen, form in relation to thorax (L=9; CI=44; RI=73): (0) conspicually larger (ovate); (1) equal to subequal; (2) abdominal syntergite I+II narrow and conspicually petiolate (Fig. 7D); (3) less; (4) fusiform.

91. Syntergite 1+2, median excavation (L=20; CI=15; RI=71): (0) until the posterior margin; (1) until 7/8 of the posterior margin; (2) until half way to the posterior margin; (3) less than half way to posterior margin.

92. Setae, organization (L=5; CI=20; RI=33): (0) Marginals, laterals, and/or discals (Fig.7B); (1) all the tergite.

93. Abdominal setae, chaetotaxy (L=6; CI=16; RI=58): (0) equal in males and females; (1) different disposition different disposition.

94. Tergite 5, form, in males (L=9; CI=33; RI=53): (0) rounded; (1) alongated (apically constricted); (2) as a conical tail (Fig. 7C); (3) with a median depression (Fig. 7B).

95. Tergite IV, ventrally in males (L=1; non-informative): (0) just setae and setulae; (1) setae, setulae and sexual patches.

96. Sternites, visibility (L=18; CI=11; RI=46): (0) all visible; (1) all invisible; (2) just sternite 1 and 2 visible.

97. Sternites, form (L=2; CI=50; RI=87): (0) as a sclerotized structure; (1) with 2 to 4 missing (as a membranous structure).

Male Terminalia

98. Tergite 6, connection with syntergosternite 7+8 (L=7; CI=57; RI=75): (0) separate (membranous) (Fig. 8A); (1) fused, but with visible suture (median dividing line present); (2) fused, but with distinguishable limits (from lateral prominences) (Fig. 8B); (3) fused, but withou distinguishable limits (from lateral prominences); (4) fused medially.

Ambiguous character. In ACCTRAN state 4 is an apomorphic homoplasy for Dufouriini + Oestrophasiini, with a resersion to state 0 in *Dufouria*. While in DELTRAN state 4 is an apomorphic homoplasy in Oestrophasiini and *Chetoptilia*.

99. Tergite 6, form (L=7; CI=57; RI=75): (0) platiform (broad) (Fig. 8A); (1) reduced to two degenerate hemitergites; (2) membranous.

Ambiguous character. In ACCTRAN state 2 is an apomorphic homoplasy for Voriini. While in DELTRAN state 2 is an apomorphic homoplasy in *Arrhinatia*, *Paedarium* + *Cyrtophleba* and *Hypovoria*.

100. Tergite 6, size in relation to syntergosternite 7+8 (L=14; CI=28; RI=61): (0) about ⅛ (Fig. 8A); (1) about the same size; (2) very narrowed (about ⅒); (3) larger; (4) about ½ (Fig. 8B).

101. Tergite 6, length in relation to segment 7+8 (L=13; CI=23; RI=58): (0) about the same size; (1) about half the size; (2) less than half the size; (3) larger.

102. Syntergosternite 7+8, form (L=8; CI=25; RI=71): (0) large, globose (Fig. 8A); (1) narrow, small; (2) large, broad (Fig. 8B).

103. Sternite 5, form in relation to membranous lateral line (L=8; CI=25; RI=57): (0) visible (Fig. 8C); (1) invisible (Fig. 8D); (2) membranous.

104. Sternite 5, lobules, development (L=11; CI=27; RI=61): (0) well developed (globose) (Fig. 8C); (1) poorly developed (internally directed); (2) poorly developed (externally directed); (3) undeveloped (Fig. 8D).

105. Sternite 5, setae, form (L=2; CI=100; RI=100): (0) with regular and short setae on apex, and without setae on base (Fig. 8C); (1) with *sensila trichodea* on base; (2) with long tuff of setae on apex.

106. Sternite 5, basally (L=6; CI=50; RI=83): (0) straight; (1) with 90º angle; (2) expanded laterally; (3) not developed.

107. Sternite 5, apically (L=3; CI=66; RI=0): (0) rounded (Fig. 8C); (1) spine like projection; (2) identate.

108. Sternite 6, fusion in relation to syntergite 7+8 (L=1; CI=100; RI=100): (0) membranous; (1) sclerotized.

109. Sternite 6, form (L=23; CI=21; RI=63): (0) asymmetrical; (1) symmetrical; (2) subsymetrical (both arms reach the same position, but the ligation with segment 7+8 is broad in one side and narrow on the other); (3) as a symmetrical plate; (4) undeveloped; (5) broad medially and narrow laterally.

Ambiguous character. In ACCTRAN state 2 is an apomorphic homoplasy for (((Eutheriini (Wagneriini + Campylochaetini)) + (Voriini (Epigrimyini + Sphatidexiini))). While in DELTRAN state 2 is an apomorphic homoplasy in Eutheriini, Wagneriini and Voriini.

110. Sternite 6, when developed, length in relation to the lobes of sternite 5 (L=3; CI=33; RI=71): (0) longer; (1) shorter.

111. Sternite 6, form in relation to segment 7 (L=2; CI=50; RI=94): (0) not superimpose; (1) superimpose at right.

Character after Tschorsnig (1985).

112. Epandrium, form (L=2; CI=50; RI=75): (0) small, somewhat straight; (1) robust, clearly globular.

113. Epandrium, specialized structures on inferior lateral margin (L=6; CI=16; RI=92): (0) lobe-like expansion (base of surstylus is somewhat hidden) (Fig. 8E); (1) without expansion (base of surstylus is not hidden) (Fig. 8F).

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for Uramyini + Dexiini. While in DELTRAN state 0 is an apomorphic homoplasy in Uramyini, *Rhamphinina* and all the remaining Dexiini, except *Stomina*.

114. Cerci, fusion (L=9; CI=22; RI=30): (0) parcial; (1) absent (free); (2) complete.

115. Cerci, spines (L=3; CI=66; RI=50): (0) just setae and setulae; (1) with spine and expansion on apex; (2) apex with spine projection.

116. Surstylus, shape (L=10; CI=40; RI=91): (0) broad, massive (Fig. 8E); (1) narrow, thin (Fig. 8F); (2) bifurcated on distal half; (3) entirely bifurcated; (4) reduced (half the size in relation to surstylus).

117. Surstylus, inclination (L=4; CI=50; RI=71): (0) posteriorly; (1) inwardly; (2) strongly sinuose.

118. Surstylus, inner side, form (L=6; CI=33; RI=95): (0) non-excavate (Fig. 8F; (1) auriculate-excavate (Fig. 8E); (2) carinate.

Character after Tschorsnig (1985).

119. Hypandrial arms (L=2; CI=50; RI=75): (0) open (Fig. 9A); (1) closed

Dorsal fusion of the hypandrium is usually found in some Exoristinae and many Tachininae (O'Hara, 2002). However, this fusion was found insome Dexiinae: *Sphatidexia* and *Trafoia*; thus, being the first obersation of the presence of this trait in Dexiinae.

120. Hypandrial apodeme, boundary with the central plate (L=12; CI=16; RI=65): (0) poorly developed (without ventral expansion); (1) developed (with ventral expansion) (Fig. 9B); (2) indistinct (Fig. 9A).

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for Wagneriini + Campylochetini. While in DELTRAN state 0 is an apomorphic homoplasy in Campylochetini, *Aldrichiopoda* + *Perisepsia*, Beskiini, *Polygaster* + *Sphatidexia*.

121. Hypandrium, central plate, length (L=1; CI=100; RI=100): (0) short; (1) elongated (Fig. 9D).

Character after Tschorsnig (1985). The elongated central plate of hipandrium was the only putative synapomorphy for Phasiinae found by Tschorsnig (1985). Here, this character state was confirmed as a synapomorphy for the Phasiinae included (*Imitomyia*, *Eutrichopoda*, *Leucostoma*, *Phasia*).

122. Hypandrium, central plate, form (L=1; CI=100; RI=100): (0) entirely sclerotized (Fig. 9B); (1) medially membranous.

123. Hypandrium, scructures (L=2; CI=50; RI=66): (0) with 3 parts delimited (hypandrial arms, central palte and apodeme) (Fig. 9B); (1) with 4 parts ((hypandrial arms, central palte, apodeme and accessory sclerite laterally).

124. Phallopodeme, intermedium, form (L=21; CI=19; RI=73): (0) spine-like process (Fig. 9C); (1) without specialization; (2) expanded laterally; (3) pad like with microtrichia; (4) large, expanded.

125. Connection between basiphallus (dorsal sclerite) and distiphallus (L=4; CI=50; RI=84): (0) membranous (Fig. 9F); (1) sclerotized; (2) partial (weak) sclerotization.

Verbeke (1962; 1963) was the first to recognize the systematic value of this characteristic, which separated his subfamilies Dexiinae, Voriinae and Dufouriinae from the other tachinids by the presence of a membranous connection between basiphallus and distiphallus. Described as "indirect and mobile "(Type II). Tschorsnig (1985) recognized this character as a putative synapomorphy of Dexiinae, which contained the tribes Dexiini, Voriini, and Dufouriini *sensu lato*. Based on this character, Wood (1987) and subsequent authors, considered Dexiinae as a possible monophyletic group within Tachinidae. However, in the first cladistic analysis of the family (Cerretti *et al*., 2014) it was recovered as a reversal in Phasiinae, not confirming the monophyly of Dexiinae. This trait supported the clade ((Dexiinae (Phasiinae + Dufouriinae)) as a synapomorphy. This putative synapomorphy of Dexiinae was also not found herein, appearing in Dexiinae and in Dufouriini sensu lato, with a reversion in Phasinae. Thus, confirming that it is a homoplastic character.

126. Membranous connection between basiphallus (dorsal sclerite) and distiphallus, 180º movement capacity (L=6; CI=16; RI=78): (0) immovable; (1) movable (Fig. 9F).

One of putative synapomorphies of Dexiinae, Voriinae and Dufouriinae (Dexiinae *sensu* Herting [1984]) suggested by Verbeke (1962; 1963) would be that the membranous connection of basiphallus (dorsal sclerite) with distiphallus would be associated with the movement capacity of distiphallus. However, some taxa with uncertain systematic position, as *Imitomyia*, have this membranous connection, but without movement (in 180°). Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for ((Dexiinae (Phasiinae + Dufouriinae)). While in DELTRAN state 1 is an apomorphic homoplasy in Dexiinae and Dufouriinae.

127. Basiphallus, length in relation to postgonite (L=10; CI=10; RI=67): (0) long; (1) short.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for ((Dexiinae (Phasiinae + Dufouriinae)). While in DELTRAN state 1 is an apomorphic homoplasy in Phasiinae, Oestrophasiini + Dufouriini and Palpostomatini.

128. Basiphallus, form (L=8; CI=50; RI=50): (0) straight to slightly curved; (1) sinuouse; (2) with basal process; (3) reduced to two symetric lobules; (4) subquadricular.

129. Basiphallus, in relation to epiphallus (L=5; CI=20; RI=89): (0) prolonged (the whole structure appers as a unit) (Fig. 9F); (1) clearly differenciated (when present).

The basiphallus being extended by the epiphallus making the entire structure appear to be a single unit is one of putative synapomorphies of Dexiinae as discussed by Tschorsnig (1985). In the present phylogenetic analysis however, this trait was not recovered as synapomorphic to Dexiinae as some tribes, e.g., Voriini and Epigrimiini, does not present this trait. On other hand, this character state was an apomorphic homoplasy for the clade (((Sophiini (Phylomiini + Thelairini)) + (Euthelotyriini (Eriotrichini (Uramyini + Dexiini)))).

130. Basiphallus, place of attachement (L=3; CI=33; RI=50): (0) basally; (1) dorsomedially.

131. Basiphallus, dorsally epiphallus (L=8; CI=12; RI=41): (0) distinct lobe (epiphallus); (1) indistinct lobe.

132. Distiphallus, form (L=13; CI=38; RI=73): (0) differenced in ventral, dorsal, and median ridge (Fig. 9F); (1) reduced (in relation to conspicuousness of scructures), very elongate, ribbon-like (Fig. 9E); (2) largely reduced, membranous (sclerotized scructures not visible); (3)

differenced just in two sclerites (posterorlly closed); (4) differenced in ventral, dorsal, and median ridge and laterally sclerotized lobes; (5) as a membrane-covered complex.

Townsend (1936) was the first to use the character state 1, distiphallus very elongate, ribbon-like, to delimitate the tribe Voriini. This trait was only used again by Verbeke (1962) to his broadly defined Voriinae: the *Voria* and *Kyrbia* groups. Following the discoveries of Verbeke (1962), Mesnil (1974) also used this trait to deliminite his Voriina (Voriini), and this was also included in Tschorsnig's (1985) dichotomous key that included besides Voriini, the subtribe Wagneriina of Mesnil (1974). The presence of this very elongate distiphallus, the longest form among the Tachinidae (Tschorsnig, 1985), was recoverd as an apomorphic homoplasy for the Voriini and appered again in *Kyrbia* and the clade *Prosopochaeta* + *Trischodischia*. Thereby, this trait is not a synapomorphy for Voriini.

133. Distiphallus, extension of the dorsal sclerite, length relative to the median ridge (L=16; CI=18; RI=65): (0) less than half; (1) somewhat shorter; (2) about same length (Fig. 9E); (3) more than a half.

134. Distiphallus, extension of the dorsal sclerite, length relative to pregonite (L=19; CI=15; RI=69): (0) equal length; (1) larger; (2) shorter (Fig. 9F); (3) very long (about 4 to 10 times longer than pregonite).

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for Campylochetini + Wagneriini. While in DELTRAN state 0 is an apomorphic homoplasy in *Aldrichiopoda* +*Perisepsia*.

135. Distiphallus, extension of the dorsal sclerite, form (L=17; CI=29; RI=65): (0) equal sized along its extension; (1) distally expanded; (2) proximally expanded; (3) as two prolongations (ventrally); (4) tubular, with multiple structures; (5) medially interrupted.

136. Distiphallus, ventral sclerite, anterior half (L=12; CI=25; RI=65): (0) entirely with microtrichia (Fig. 10A); (1) bare, with weak scleratization; (2) bare, with strong scleratization; (3) entirely bare.

137. Distiphallus, anterior portion (L=10; CI=20; RI=66): (0) dorsal sclerite with equal width in relation ventral sclerite (Fig. 10A); (1) expanded; (2) greatly expanded (with sclerotized ring); (3) lateral lobes.

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for ((Dexiinae (Phasiinae + Dufouriinae)). While in DELTRAN state 0 is an apomorphic homoplasy in Dexiinae.

138. Distiphallus, ventral sclerite, in relation to median ridge (L=10; CI=30; RI=6653 (0) fused; (1) fused, with boundaries visible; (2) not fused (isolated); (3) broad (envolving all distiphallus).

139. Distiphallus, ventral sclerite, in relation to dorsal sclerite (L=22; CI=18; RI=64): (0) fused partially (dorsal portion); (1) not fused; (2) fused without microtichia; (3) fused with microtrichia; (4) longer.

140. Distiphallus, ventral sclerite, extension (L=7; CI=57; RI=50): (0) laterally with distiphallus; (1) begins in basiphallus, ending in the distiphallus; (2) about ¼ posteriorly in relation to basiphallus; (3) ventrally to basiphallus; (4) beyond the extension of basiphallus.

141. Distiphallus, acrophallus, form (L=25; CI=20; RI=73): (0) reduced as a small somewhat sclerotized structure; (1) as a granular structure (Fig. 10A); (2) globose expansion; (3) undeveloped; (4) expanded with microthricia; (5) membranous.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for ((Eutheriini (Wagneriini + Campylochaetini)). While in DELTRAN state 1 is an apomorphic homoplasy in Eutheriini and *Kyrbia*.

142. Distiphallus, granular structure of acrophallus, length in relation to extension of the dorsal sclerite (L=16; CI=18; RI=68): (0) about equal length; (1) larger, about more than the double (Fig. 10A); (2) shorter, about half the size; (3) shorter, about ⅒.

143. Distiphallus, surface (L=3; CI=33; RI=90): (0) with microtrichia; (1) bare.

144. Pregonite connection in relation to postgonite (L=4; CI=50; RI=85): (0) not fused (Fig. 10D); (1) fused with seam; (2) fused without seam (Fig. 10C).

145. Pregonite, insertion in the hypandrial arms (L=1; CI=100; RI=100): (0) anterior (Fig. 10D); (1) posterior.

146. Pregonites, fusion (L=6; CI=50; RI=75): (0) separated from each other; (1) partially fused; (2) fully fused (Fig. 10C); (3) fused, encircling phallapodem.

147. Pregonite, in relation middle plate of hypandrium (L=18; CI=11; RI=78): (0) fused medially; (1) fused completely; (2) not fused.

148. Pregonite, in relation to hypandrium (L=2; CI=50; RI=83): (0) ends at the base of the central plate; (1) goes beyond the central plate.

149. Pregonite, ventrally (L=2; CI=50; RI=80): (0) straight (Fig. 10D); (1) protuberance with setulae.

150. Pregonite, form (L=15; CI=40; RI=88): (0) platiform, with strong sclerotifization anteriorly (distally expanded) (Fig. 10D); (1) platiform, with equal sclerotifization (equal size); (2) platiform, medially expanded; (3) lobe-like; (4) elongated, encircling the phalopodem; (5) subquadricular (expanded laterally); (6) with spine distally (lobe-like).

One of the most quoted and discussed putative synapomorphy of Dexiinae, in addition to the basiphallus extended by the epiphallus (129: 0) and membranous connection between basiphallus and distiphallus (125: 0), is the presence of a platiform pregonite (150: 0) as hinted by Tschorsnig (1985). First of all, while scoring this character state it became clear that this is not a single trait, hence, “platiform” is herein contructed as 3 differente character states: platiform, with strong sclerotifization anteriorly (distally expanded) (150: 0), platiform, with equal sclerotifization (equal size) (150: 1) and platiform, medially expanded (150: 2).

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for ((Dexiinae (Phasiinae + Dufouriinae)). While in DELTRAN state 1 is an apomorphic homoplasy in Dexiinae. Hence, a platiform, with equal sclerotifization is the apomorphic state found only in Dexiinae (excluding Dufouriinae).

151. Pregonite, direction, when platiform (L=14; CI=14; RI=76): (0) strong downward directed (forming a straight angle) (Fig. 10D); (1) weak downward directed (less than a straight angle); (2) straight.

152. Pregonite, surface (L=8; CI=12; RI=53): (0) with microtrichia; (1) bare.

153. Postgonite, anterior margin, sclerotization (L=1; CI=100; RI=100): (0) strong; (1) weak (Fig. 10B).

154. Postgonite, poterior margin, position (L=1; non-informative): (0) below the hypandrial arms; (1) above the hypandrial arms.

155. Postgonite, position with the pregonite (L=3; CI=66; RI=66): (0) not articulated; (1) articulated; (2) overlapped.

156. Postgonite, posterior region, form (L=17; CI=41; RI=72): (0) concave, crescent moon (along the basiphallus) (Fig. 10A); (1) subretanctular; (2) subretanctular with ventral spine like spurs; (3) expanded anteriorly and narrow posteriorly; (4) rod like (expanded anteriorly); (5) lobe-like; (6) rectangular with posterior projection; (7) globular, with posterior margim narrow (Fig. 10B).

157. Postgonite, surface (L=1; CI=100; RI=100): (0) with microtrichia; (1) bare.

Female terminalia

158. Sternite 5, form (L=3; CI=33; RI=33): (0) unmodified (rectangular with regular setae); (1) modified (strong setae apically); (2) reduced.

159. Tergite 6, sclerotization (L=2; CI=50; RI=0): (0) well developed; (1) wholly membranous.

160. Tergite 6, form, when sclerotized (L=7; CI=57; RI=40): (0) short (Fig. 11A); (1) broad, twice larger in comparison with other tergites (Fig. 12B); (2) broad, somewhat larger in comparison with other tergites; (3) tube-like; (4) fused with sternite 6; (5) strong spine, bearing 3 stout blunt.

161. Tergite 6, dorsally (L=9; CI=11; RI=46): (0) unidivided plate (Fig. 11B); (1 as two broad lateral plates.

162. Tergite 6, surface (L=1; non-informative): (0) setulose; (1) with paired rounded structures with long setae.

163. Sternite 7, in relation to a single piece (L=3; CI=66; RI=0): (0) complete dorsally (Fig. 11A); (1) entirely membranous; (2) broad ventrally and incomplete dorsally.

164. Tergite 7, in relation to a single piece (L=14; CI=12; RI=50): (0) complete dorsally (Fig. 11A); (1) as 2 broad plates; (2) wholly membranous; (3) as two small sclerites.

165. Tergite 8 (L=12; CI=8; RI=82): (0) present (clearly differenciated from other structures) (Fig. 11C); (1) indistinct.

166. Tergite 8, shape, when isolated (L=7; CI=42; RI=75): (0) wide plate (Fig. 12A); (1) narrow lateral strip (Fig. 12B); (2) V-shaped (strongly sclerotized apically); (3) divided as two lateral plates; (4) piercer.

167. Tergite 8, in relation to a single piece (L=8; CI=25; RI=72): (0) complete dorsally; (1) incomplete dorsally; (2) rudimentary (membranous with setae).

168. Tergite 8, fusion (L=6; CI=50; RI=76): (0) with sternite 8 (Fig. 11C); (1) with sternite 9 (Fig. 12A); (2) not fused; (3) fused with tergite 7.

Ambiguous character. In ACCTRAN optimization state 1 is an apomorphic homoplasy for Uramyini, but as this trait is inapplicable for *Trafoia*, *Blepharomyia*, *Prosopochaeta*, *Trischodischia* and *Eulasiona*; thus that apomorphy is spurious. In DELTRAN this state becomes a synapomorphy for Thelairaporia and Uramyia, representing the codification for that character, so it was used.

169. Tergite 8, form of the fusion with sternite 8 (L=1; non-informative): (0) cone shape (posteriorly facing) (Fig. 11A); (1) peak shape (ventrally facing).

170. Sternite 8, duplication (L=1; CI=100; RI=100): (0) single piece; (1) paired piece.

171. Sternite 8, form (L=17; CI=41; RI=66): (0) subsquared (narrow strip) (Fig. 11B); (1) spatulate (Fig. 12A); (2) conical shape; (3) distally divided in two lobes; (4) deeply grooved with lightly sclerotized extension; (5) subsquared (narrow strip) with median rounded projection; (6) spoon-like; (7) broad anteriorly and very narrow posteriorly (piercer) (Fig. 12B); (8) sharp and short.

Ambiguous character. In ACCTRAN state 2 is an apomorphic homoplasy for Dufouriinae; and state 1 is a synapomorphy for Epigrimyini and Sphatidexiini. While in DELTRAN state 2 is a homoplasy in Freraea and in Dufouriini; state 1 is a synapomorphy for *Polygaster* + *Sphatidexia*.

172. Sternite 8, surface (L=14; CI=14; RI=73): (0) setulae in all surface; (1) setulae just apically; (2) bare.

173. Syntergite 9 + 10 (L=4; CI=25; RI=40): (0) present (clearly differenciated from other structures); (1) Indistinct.

Dexiinae was defined by Herting (1957) on the absence of syntergite 9+10 (his end tergite). This inference was confirmed herein as no member of Dexiinae, or even Dufouriinae, presents this structure.

174. Sternite 10, form (L=8; CI=50; RI=66): (0) subsquare (Fig. 11B); (1) elongated (as long as tergite 7); (2) narrow and short (shorter than tergite 7); (3) reduced, partially membranous; (4) entirelly membranous; (5) fused with lingulae.

175. Sternite 9, form (L=1; CI=100; RI=100): (0) well developed; (1) undeveloped.

176. Sternite 9, length (L=5; CI=40; RI=81): (0) elongated (longer than sternite 8) (Fig. 11A); (1) short (shorter or equal size than sternite 8) (Fig. 11C); (2) elongated, same length as the long and modified sternite 8 (Fig. 12A).

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for Dufouriinae. While in DELTRAN state 0 is an apomorphic homoplasy in Frearaeini and Dufouriini.

177. Sternite 9, in relation to a single piece (L=3; CI=66; RI=83): (0) as a simple paired structure; (1) as a duplicated structure (one anterior and one posterior); (2) piercer (long and sharp) about 5X the length of tergite 6 (Fig. 12A); (3) piercer (short and sharp) at most 2X the length of tergite 6.

178. Number of spermatheca (L=1; CI=100; RI=100): (0) 3; (1) 2.

179. Surface (L=28; CI=10; RI=69): (0) striated; (1) low roughness; (2) high roughness; (3) smooth.

Ambiguous character. In ACCTRAN state 1 is an apomorphic homoplasy for ((Dexiinae (Phasiinae + Dufouriinae)). While in DELTRAN state 1 is an apomorphic homoplasy in Phasiinae and Dufouriini + Oestrophasiini.

EGG

180. Eggs (L=7; CI=42; RI=33): (0) membranous; (1) macrotype (Fig. 15B); (2) microtype (Fig. 15A); (3) membranous with longitudinal depression.

Egg types are traditionally used for delineation of some groups, e.g., macrotype in some tribes in Phasiinae and Exoristini, microtype in Goniini and membranous for Tachininae and Dexiinae (Herting, 1960; Gaponov, 2003). Macrotype eggs are characterized by being relatively large (greater than 0.4 mm) and flat-convex, i.e., the dorsal surface usually contains a polygonal network, while the ventral surface is smooth and contains adherent substances (to be glued to the body host), the first instar larva is not incubated (developing while adhered to the host); usually, these eggs are present in some tribes of the Phasiinae and Exoristinae. However, for the first time - as a result of dissections made herein - two genera was discovered to present a macrotype egg: *Polygastroptery* and *Trichodischia*.

181. Form (L=4; CI=50; RI=50): (0) without specialization (smooth); (1) polygonal surface (Fig. 15B); (2) posterodorsal window.

LARVA

First instar larva

182. Dermal cuticle, shape (L=10; CI=60; RI=94): (0) dark-colored scales; (1) weakly sclerotized cuticular plates (Fig. 14A); (2) small irregular plates; (3) just spiniform/microtrichia (Fig. 14B); (4) cuticle striated with microtrichia; (5) small and subrectangular plates dorsally (Fig. 14B); (6) entirely bare.

The type of dermal cuticle comprises important biological characteristics in relation to the strategy of host infection. State 0 is found in *Archytas* and *Irengia* in addition to all species that perform the sit-and-wait strategy to find its host (mainly Tachinini), which is often a caterpillar, and as soon as it finds it, the host is infected, and the larva does not suffer desiccation while waiting because the presence of the dermal plates. Since the discussion made by Thompson (1963), the state 1 was considered as a derived state for Dexiini (Richter &

Farinets, 1983); this reflects the strategy of actively seek their host, mostly larvae of beetles; such scale-like plates bears spines that assist the search for the host by providing friction against the substrate, which may be in the ground or within trunks (Barraclough, 1992). Herein, this trait was found to be synapomorphic for Dexiini. State 2 is found in other tachinids, which are larvae that do not undergo major morphological modifications, possessing several other forms of host infection.

183. Weakly sclerotized cuticular plates, chaetotaxy (L=11; CI=36; RI=56): (0) with spines; (1) bare; (2) bare, but with spines just in segment IX-X; (3) bare, but with spines just in segment XII; (4) bare, but with spines just in segment XII.

184. Weakly sclerotized cuticular plates, chaetotaxy, type (L=5; CI=60; RI=33): (0) short spines posteriorly; (1) short spines posteriorly (segment II-XI) and long spines (just segment XII); (2) short, long and platelets spines; (3) short spines, and heavier spines (broad) posteriorly.

185. Weakly sclerotized cuticular plates, spines, location (L=8; CI=25; RI=53): (0) segment III; (1) segment II-XI; (2) Segment II-XII.

186. Weakly sclerotized cuticular plates, form (L=15; CI=26; RI=77): (0) transverse (elongate-oval) (Fig. 14F); (1) polygonal (Fig. 14C); (2) rectangular (Fig. 14E); (3) subsquared (Fig. 14D); (4) rounded platelets.

187. Weakly sclerotized cuticular plates, distribution in relation to a single segment (L=9; CI=11; RI=42): (0) all the segment; (1) just anterior portion.

188. Integument (L=13; CI=7; RI=80): (0) sensila; (1) just microtichia.

189. Segment I, antenna (L=10; CI=20; RI=83): (0) present and well developed (Fig. 14A); (1) present, but reduced; (2) invisible.

190. Segment I, antenna, shape (L=12; CI=16; RI=83): (0) flattened; (1) conic (Fig. 14A); (2) somewhat elongate.

Ambiguous character. In ACCTRAN state 2 is an apomorphic homoplasy for (((Eutheriini (Wagneriini + Campylochaetini)) + (Voriini (Epigrimyini + Sphatidexiini))). While in DELTRAN state 1 is an apomorphic homoplasy in *Beskia* and Voriini.

191. Segment I, recurved cephalic organ (L=11; CI=18; RI=86): (0) well developed (clavate) (Fig. 14A); (1) not developed (invisible); (2) slightly developed.

Ambiguous character. In ACCTRAN state 2 is an apomorphic homoplasy for (((Eutheriini (Wagneriini + Campylochaetini)) + (Voriini (Epigrimyini + Sphatidexiini))). While in DELTRAN state 2 is an apomorphic homoplasy in Sphatidexiini and Voriini.

192. Ventrally (L=3; CI=66; RI=88): (0) microtrichia; (1) long spine-like microtrichia; (2) strong and darkened microtrichia.

193. Segment II-IX, form (L=7; CI=28; RI=50): (0) spines-like projection; (1) just microtrichia; (2) just segment II-III.

Ambiguous character. In ACCTRAN state 0 is an apomorphic homoplasy for *Rhamphina* and all other Dexiini except *Stomina*. While in DELTRAN state 1 is an apomorphic homoplasy in *Rhamphina* and *Doleschalla*.

194. Segment V, microtrichia, localization (L=4; CI=50; RI=50): (0) dorsal and ventral; (1) ventral; (2) dorsal.

195. Segment XII, shape (L=14; CI=28; RI=64): (0) rounded (Fig. 13A); (1) conic (Fig. 13C); (2) various prolongations; (3) lateral prolongation; (4) elongate and conical.

196. Segment XII specializations (L=2; CI=50; RI=0): (0) not divided; (1) divided or with pseudopods.

197. Segment X, form (L=2; CI=100; RI=100): (0) microtrichia; (1) stylus; (2) bare.

198. Segment XI, form of microtrichia (L=2; CI=50; RI=50): (0) small; (1) sensorial stylus (Fig. 13C); (2) spine-like microtrichia.

199. Segment XII, from of microtrichia (L=17; CI=17; RI=65): (0) small; (1) sensorial stylus (Fig. 13B); (2) long spine-like microtrichia; (3) bare.

200. Segment XII, number of sensorial stylus (L=10; CI=30; RI=56): (0) 1 pair (Fig. 13C); (1) 2 pairs; (2) 3 pairs; (3) 4 pairs.

201. Posterior spiracle, slits shape (L=6; CI=66; RI=92): (0) rounded (Fig. 14A); (1) vestigial (reduced) (Fig. 13A); (2) undeveloped (apneustic); (3) round with darkened and broad borders (Fig. 13D); (4) transversal.

Ambiguous character. In ACCTRAN state 3 is an apomorphic homoplasy for (((Eutheriini (Wagneriini + Campylochaetini)) + (Voriini (Epigrimyini + Sphatidexiini))). While in DELTRAN state 3 is an apomorphic homoplasy in Sphatidexiini and Voriini.

202. Posterior spiracle, felt chambers, form (L=3; CI=66; RI=95): (0) entirely transparent (Fig. 14A); (1) distal portion darkened (Fig. 13D); (2) reduced (invisible).

203. Posterior spiracle, felt chambers, protrusion (L=29; CI=6; RI=68): (0) at the level of the cuticle (not visible) (Fig. 14A); (1) a little protrusion; (2) tubular process (Fig. 13C).

Cephaloskeleton

204. Mandibles (L=1; non-informative): (0) present; (1) fused, invisible.

205. Labrum (L=1; non-informative): (0) normally developed; (1) strongly developed.

206. Sclerit of the salivary gland, shape (L=26; CI=30; RI=79): (0) reduced to a narrow strip; (1) narrow anteriorly, wide posteriorly (Fig. 13A); (2) wide anteriorly, narrow posteriorly (Fig. 13B); (3) rounded anteriorly and narrow posteriorly; (4) rectangular; (5) subsquared; (6) falciform; (7) elongate clavate strip; (8) narrow with base enlarged.

207. Mouth hook, shape (L=16; CI=18; RI=80): (0) truncate apically (Fig. 13B); (1) unciform; (2) unciform, but apical medial region pointed; (3) large, quadrate; (4) arrow-like.

208. Posterior portion of the cephalic skeleton (L=1; CI=100; RI=100): (0) differentiated in dorsal and ventral cornua; (1) undifferentiated.

209. Accessory sclerite, position with regard to sclerite of the salivary gland (L=3; CI=33; RI=33): (0) ventral; (1) dorsoventrally.

210. Intermediate region, form (L=4; CI=25; RI=70): (0) with median enlargement; (1) same width along its extension (Fig. 14B).

211. Dorsal horn, length compared to intermediate region (L=4; CI=50; RI=33): (0) longer; (1) shorter; (2) narrow and shorter.

212. Dorsal horn, in relation to ventral horn (L=14; CI=7; RI=58): (0) both straight; (1) ventral curved and dorsal straight.

Appendix 2. Morphological character matrix showing 212 characters for 163 terminals including 13 outgroups. Inapplicable and missing character states are coded “–” and "?", respectively.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Calliphora vomitoria	1	0	0	0	0	1	1	0	0	0	0	1	0	0	-	0	0	1	1	1	1	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	1	0	1	1
Polygaster brasiliensis	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0
Polygaster sp	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0
Spathidexia brasiliensis	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0
Spathidexia dunningii	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0
Spathidexia spatulata	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0
Parodomyiops thelairopods	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	0	1	2	0	0	1	1	0	0	0
Allothelaira diaphana	1	0	0	0	0	1	1	1	0	0	0	1	1	0	-	0	0	1	1	0	0	-	0	0	0	0	1	0	0	1	1	1	2	0	0	1	1	0	0	0
Thelaira americana	1	0	0	0	0	1	1	0	0	0	0	1	1	0	-	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	2	0	0	1	1	0	0	0
Thelaira nigripes	1	0	0	0	0	1	1	0	0	0	0	1	0	0	-	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	2	0	0	1	1	0	0	0
Thelairodes vittigera	0	0	0	0	0	1	1	0	0	0	0	1	0	1	-	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	2	0	0	1	1	0	0	0
Torocca munda	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Torocca fasciata	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Xanthodexia sericea	1	0	0	0	1	0	1	1	0	0	0	0	0	0	-	2	1	0	1	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Halydaia luteicornis	0	0	0	0	1	1	1	0	0	1	0	1	2	1	3	1	4	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0
Polygastropteryx	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	1	0	0	1	1	0	0	2
Eulasiona comstocki	1	0	1	0	0	1	1	0	0	1	0	0	0	0	-	0	0	1	0	0	2	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0
Kirbya moerens	1	0	0	0	1	1	1	0	0	0	0	1	0	0	-	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0
Aldrichiopa coracella	1	0	1	0	1	1	1	1	0	0	0	1	0	1	1	2	1	1	1	1	2	1	0	0	0	0	1	1	1	2	1	0	0	1	1	0	1	0	1	1
Rhamphina pedemontana	1	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	-	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	2	0
Stomina tachinoides	1	0	0	0	1	1	1	0	0	0	0	1	0	0	-	0	0	0	1	1	0	-	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1	0	1	0
Doleschalla elongata	1	0	0	1	0	1	1	0	1	1	1	0	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	1	-	0
Doleschalla consobrina	1	0	0	1	0	0	1	0	1	1	1	0	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	1	-	0
Campylocheta lipernis	0	0	1	0	2	1	1	0	0	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	1	1	2	0	1	0	1	0	1	1	0	0	1
Campylocheta praecox	0	0	1	0	2	1	1	0	0	1	0	1	0	0	-	0	0	0	0	0	1	-	0	0	0	0	1	1	1	2	0	1	0	1	0	0	1	0	0	1
Campylocheta townsendi	0	0	1	0	2	1	1	0	0	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	1	1	2	0	1	0	1	0	1	1	0	0	1
Parahypochaeta genalis	0	0	0	0	1	1	1	0	0	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	1	1	2	0	1	0	1	0	1	1	0	0	1
Phyllomya volvulus	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	-	0	0	0	0	0	0	1	1	0	1	2	0	0	0	1	0	0	0
Leptothelaira longicauda	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	1	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Cyrtophleba nigripalpis	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	0	0	2	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0
Plagiomima spinolusa	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	1	0	2	-	0	0	0	0	1	0	1	1	0	1	0	1	1	1	1	0	0	0
Arrhinactia cylindrica	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0
Athrycia cinerea	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0
Cyrtophleba sp	0	0	1	0	0	1	1	1	0	0	0	1	0	1	2	2	1	0	1	0	2	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0
Cyrtophleba ruricola	0	0	1	0	0	1	1	1	0	0	0	1	0	1	2	2	1	0	1	0	2	0	0	0	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0

(continued)

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Calliphora vomitoria	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Polygaster brasiliensis	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	2	2	-	0	0	0	0	0	0	0	0	1	1	1	2	0	1
Polygaster sp	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	2	2	-	0	0	0	0	0	0	0	0	1	1	1	2	0	1
Spathidexia brasiliensis	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	2	1	-	0	0	0	0	0	3	0	0	0	1	1	1	0	0
Spathidexia dunningii	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	2	1	-	0	0	0	0	0	3	0	0	0	1	1	1	0	0
Spathidexia spatulata	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	2	1	-	0	0	0	0	0	3	0	0	0	1	1	1	0	0
Parodomyiops thelairopods	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	2	-	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Allothelaira diaphana	1	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	2	2	-	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Thelaira americana	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	1	-	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Thelaira nigripes	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	1	-	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Thelairodes vittigera	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	2	-	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Torocca munda	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0
Torocca fasciata	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0
Xanthodexia sericea	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	2	2	-	0	0	2	0	0	0	0	0	0	1	1	1	0	0
Halydaia luteicornis	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	2	2	-	0	0	0	0	0	0	0	0	0	1	1	2	1	1
Polygastropteryx bicoloripes	-	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	2	-	0	0	0	0	0	0	0	0	0	1	1	2	1	1
Eulasiona comstocki	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Kirbya moerens	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	2	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Aldrichiopa coracella	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	2	0	0	0	0	1	1	1	-	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Rhamphina pedemontana	0	1	0	1	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0	0	0	0	0	3	0	0	0	1	1	0	0	0
Stomina tachinoides	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	-	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Doleschalla elongata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Doleschalla consobrina	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Campylocheta lipernis	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Campylocheta praecox	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Campylocheta townsendi	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Parahypochaeta genalis	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Phyllomya volvulus	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	2	-	0	0	0	0	0	2	0	0	0	1	1	0	0	0
Leptothelaira longicauda	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	2	-	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Cyrtophleba nigripalpis	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	2	1	0
Plagiomima spinolusa	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0
Arrhinactia cylindrica	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	1	0
Athrycia cinerea	1	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0
Cyrtophleba sp	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	2	-	0	0	0	0	0	0	0	0	0	1	1	2	1	0
Cyrtophleba ruricola	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	2	0	0

(continued)

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Calliphora vomitoria	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Polygaster brasiliensis	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	2	0	2	2	1	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0
Polygaster sp	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	2	0	2	2	1	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0
Spathidexia brasiliensis	0	1	0	1	0	0	0	0	0	1	3	0	0	0	0	1	0	2	0	2	2	1	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	0
Spathidexia dunningii	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	2	0	2	2	1	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	0
Spathidexia spatulata	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	2	0	2	2	1	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	0
Parodomyiops thelairopods	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Allothelaira diaphana	0	1	0	1	1	1	0	0	0	1	3	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Thelaira americana	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Thelaira nigripes	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Thelairodes vittigera	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Torocca munda	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	1	0	0	0	0	0	2	3	0	3	0	0	4	-	0	0	1	1	0	1	1	0	0	1
Torocca fasciata	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	4	-	0	0	1	1	0	1	1	0	0	1
Xanthodexia sericea	0	1	0	1	1	1	0	0	0	1	3	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	1
Halydaia luteicornis	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1
Polygastropteryx bicoloripes	0	1	0	1	1	0	0	0	0	4	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	1	1	0	1	0	0	0	1
Eulasiona comstocki	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Kirbya moerens	3	1	0	1	0	0	0	0	0	4	0	0	0	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Aldrichiopa coracella	3	1	0	1	0	0	0	0	0	4	3	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0	2	0	1	0	1	1	0	1	0	2	0	0
Rhamphina pedemontana	2	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
Stomina tachinoides	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
Doleschalla elongata	0	1	0	1	1	0	0	0	1	3	3	0	0	2	0	1	1	0	2	-	0	0	0	0	0	3	0	0	1	0	0	0	0	1	0	0	0	1	0	1
Doleschalla consobrina	0	1	0	1	1	0	0	0	1	3	3	0	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1
Campylocheta lipernis	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	2	0	1	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Campylocheta praecox	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	2	0	1	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Campylocheta townsendi	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	2	0	1	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Parahypochaeta genalis	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	2	0	1	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Phyllomya volvulus	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1
Leptothelaira longicauda	0	1	0	1	1	0	0	0	0	4	3	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Cyrtophleba nigripalpis	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Plagiomima spinolusa	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	2	1	0	0	0	3	0	0	0	0	1	0	1	1	0	1	0	2	0	1
Arrhinactia cylindrica	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	2	0	0	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Athrycia cinerea	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	-	-	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Cyrtophleba sp	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Cyrtophleba ruricola	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0	-	0	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1

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Species	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Calliphora vomitoria	0	0	0	0	1	0	1	4	1	1	0	4	3	1	2	0	3	1	4	4	5	-	0	0	0	0	2	0	0	6	-	0	0	0	1	4	0	0	0	0
Polygaster brasiliensis	0	1	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1	3	4	-	0	0	0	0	0	0	1	1	2	0	0	0	1	3	0	0	0	0
Polygaster sp	0	1	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1	3	4	-	0	0	0	0	0	0	1	1	2	0	0	0	1	3	0	0	0	0
Spathidexia brasiliensis	0	1	0	1	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1	3	4	-	0	0	0	0	2	0	1	1	2	0	0	0	1	3	0	0	0	0
Spathidexia dunningii	0	1	0	1	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	2	0	0	0	1	3	0	0	0	0
Spathidexia spatulata	0	1	0	1	0	1	0	0	0	0	1	0	0	1	2	0	0	0	1	3	4	-	0	0	0	0	2	0	1	1	2	0	0	0	1	3	0	0	0	0
Parodomyiops thelairopods	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	5	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Allothelaira diaphana	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	4	3	-	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Thelaira americana	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	3	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Thelaira nigripes	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	3	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Thelairodes vittigera	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	5	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Torocca munda	0	0	0	0	0	1	0	0	0	0	0	0	2	1	1	1	0	2	0	0	1	2	0	0	0	0	2	0	0	1	1	1	0	0	1	0	0	0	0	0
Torocca fasciata	0	0	0	0	0	1	0	0	0	0	0	0	2	1	1	1	0	2	2	0	1	2	0	0	0	0	2	0	0	1	1	1	0	0	1	0	0	0	0	0
Xanthodexia sericea	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	1	0	1	2	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Halydaia luteicornis	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	4	1	1	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Polygastropteryx bicoloripes	0	0	0	1	1	0	1	4	1	1	0	4	0	1	3	2	1	1	2	4	4	-	0	0	0	0	2	0	0	3	-	0	0	0	1	4	0	0	0	0
Eulasiona comstocki	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	2	0	3	-	0	0	0	0	1	0	0	0	2	1	0	0	1	0	0	0	1	0
Kirbya moerens	0	0	0	0	0	1	0	0	1	0	0	1	2	3	0	0	1	0	1	0	3	-	1	0	0	1	0	0	0	4	-	1	0	0	1	1	0	0	0	0
Aldrichiopa coracella	0	0	0	1	0	1	0	0	0	0	0	2	1	0	0	0	0	0	2	0	5	-	1	0	0	0	1	0	0	4	-	1	0	0	1	1	0	0	0	0
Rhamphina pedemontana	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Stomina tachinoides	0	0	0	0	0	1	0	0	0	0	0	3	2	1	0	0	0	0	3	0	3	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Doleschalla elongata	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Doleschalla consobrina	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Campylocheta lipernis	0	0	0	3	0	0	1	0	0	0	0	0	2	2	0	0	0	0	2	0	2	-	0	0	0	3	1	0	0	3	-	1	0	0	1	2	0	0	0	0
Campylocheta praecox	0	0	0	3	0	0	1	0	0	0	0	0	2	2	0	0	0	0	2	0	2	-	0	0	0	3	1	0	0	3	-	1	0	0	1	2	0	0	0	0
Campylocheta townsendi	0	0	0	3	0	0	1	0	0	0	0	0	2	2	0	0	0	0	2	0	2	-	0	0	0	3	1	0	0	3	-	1	0	0	1	2	0	0	0	0
Parahypochaeta genalis	0	0	0	3	0	0	1	0	0	0	0	0	2	2	0	0	0	0	2	0	2	-	0	0	0	3	1	0	0	3	-	1	0	0	1	2	0	0	0	0
Phyllomya volvulus	0	0	0	0	0	1	0	0	0	0	0	0	2	1	1	2	0	0	0	0	5	-	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Leptothelaira longicauda	0	0	0	0	0	1	0	0	0	0	0	0	2	0	1	2	0	0	0	0	5	-	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
Cyrtophleba nigripalpis	0	0	0	0	0	1	1	0	1	0	0	1	2	1	0	0	0	0	1	0	3	-	1	0	0	0	1	0	0	4	-	1	0	0	1	2	0	0	0	0
Plagiomima spinolusa	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	1	0	1	0	3	-	1	0	0	1	0	0	0	4	-	1	0	0	1	0	0	0	0	0
Arrhinactia cylindrica	0	0	1	0	0	1	1	0	1	0	0	1	2	1	0	0	0	0	1	0	5	-	1	0	0	0	1	0	0	4	-	1	0	0	1	1	0	0	0	0
Athrycia cinerea	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	3	-	1	0	0	0	0	0	0	4	-	1	0	0	1	0	0	0	0	0
Cyrtophleba sp	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	5	-	1	0	0	0	0	0	0	1	-	1	0	0	1	1	0	0	0	0
Cyrtophleba ruricola	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	5	-	1	0	0	1	0	0	0	1	-	1	0	0	1	0	0	0	0	0

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Species	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Calliphora vomitoria	0	0	0	0	0	3	1	2	-	0	2	0	1	0	0	1	0	0	1	3	-	3	-	-	-	-	-	1	0	1	0	0	0	0	0	0	0	0	0	-
Polygaster brasiliensis	0	0	0	0	0	0	1	1	-	1	1	1	1	0	?	2	2	0	2	0	0	3	-	-	-	-	-	0	0	0	2	0	1	0	0	0	0	0	0	-
Polygaster sp	0	0	0	0	0	0	1	1	-	1	1	1	1	0	0	2	2	0	2	0	0	3	-	-	-	-	-	0	0	0	2	0	1	0	0	0	0	0	0	-
Spathidexia brasiliensis	0	0	0	0	0	0	1	1	-	1	1	1	1	0	0	2	2	0	2	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Spathidexia dunningii	0	0	0	0	0	0	1	1	-	1	1	1	1	0	0	2	2	0	2	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Spathidexia spatulata	0	0	0	0	0	0	1	1	-	1	1	1	1	0	0	2	2	0	2	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Parodomyiops thelairopods	0	0	0	0	0	1	2	2	-	0	6	1	1	0	0	2	0	0	1	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Allothelaira diaphana	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	1	2	2	1	0	0	0	0	0	0	-
Thelaira americana	1	0	0	1	1	-	-	-	-	0	6	1	1	0	0	2	0	0	3	0	0	3	-	-	-	-	-	1	1	1	2	2	1	0	0	0	0	0	0	-
Thelaira nigripes	1	0	0	1	1	-	-	-	-	0	6	1	1	0	0	2	0	0	3	0	0	3	-	-	-	-	-	1	1	1	2	2	1	0	0	0	0	0	0	-
Thelairodes vittigera	0	0	0	0	0	1	2	2	-	0	6	1	1	0	0	2	0	0	1	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Torocca munda	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	-	0	0	3	-	-	-	-	-	1	1	0	0	0	0	0	0	0	0	0	0	-
Torocca fasciata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	-	0	0	3	-	-	-	-	-	1	1	0	0	0	0	0	0	0	0	0	0	-
Xanthodexia sericea	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	1	1	1	2	0	1	0	0	0	0	0	0	-
Halydaia luteicornis	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	1	2	0	1	0	0	0	0	0	0	-
Polygastropteryx bicoloripes	1	0	0	1	0	0	0	2	-	0	0	0	1	0	0	1	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eulasiona comstocki	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kirbya moerens	0	0	0	1	0	1	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aldrichiopa coracella	0	0	0	0	0	0	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	0	1	0	1	0	0	0	0	0	0	-
Rhamphina pedemontana	1	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	2	0	0	2	1	1	1	0	2	0	0	0	2	1	0	0	0	1	0
Stomina tachinoides	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	2	0	0	2	2	1	1	1	0	1	0	1	2	0	0	0	0	1	1
Doleschalla elongata	0	0	0	0	1	-	0	2	-	0	0	0	1	0	0	1	0	0	3	0	0	2	0	0	2	1	0	0	0	2	0	0	0	0	4	0	0	0	1	0
Doleschalla consobrina	0	0	0	0	1	-	2	2	-	0	0	0	1	0	0	1	0	0	3	0	0	2	0	0	2	1	0	0	0	2	0	0	0	0	4	0	0	0	1	0
Campylocheta lipernis	0	0	0	1	0	0	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	0	0	1	0	1	0	0	0	0	0	0	-
Campylocheta praecox	0	0	0	1	0	0	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	0	0	1	0	1	0	0	0	0	0	0	-
Campylocheta townsendi	0	0	0	1	0	0	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	0	0	1	0	1	0	0	0	0	0	0	-
Parahypochaeta genalis	0	0	0	1	0	0	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	0	0	1	0	1	0	0	0	0	0	0	-
Phyllomya volvulus	0	0	0	1	1	-	-	-	-	0	6	0	1	0	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	0	2	2	1	1	0	0	0	0	3	-
Leptothelaira longicauda	0	0	0	0	1	-	-	-	-	0	6	0	1	0	0	1	0	0	?	0	0	3	-	-	-	-	-	1	0	0	2	?	1	?	?	?	?	?	?	?
Cyrtophleba nigripalpis	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	3	0	0	0	0	-
Plagiomima spinolusa	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Arrhinactia cylindrica	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Athrycia cinerea	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	0	1	0	0	1	0	0	0	0	0	0	-
Cyrtophleba sp	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	3	0	0	0	0	-
Cyrtophleba ruricola	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	3	0	0	0	0	-

(continued)

Species	201	202	203	204	205	206	207	208	209	210	211	212
Calliphora vomitoria	0	0	0	0	0	1	-	0	0	0	1	1
Polygaster brasiliensis	2	0	1	1	1	1	3	1	1	1	1	0
Polygaster sp	2	0	1	1	1	1	3	1	1	1	1	0
Spathidexia brasiliensis	2	0	1	1	1	1	3	0	1	1	1	1
Spathidexia dunningii	2	0	1	1	1	1	3	0	1	1	1	1
Spathidexia spatulata	2	0	1	1	1	1	3	0	1	1	1	1
Parodomyiops thelairopods	1	0	0	1	1	7	0	0	1	1	1	0
Allothelaira diaphana	0	0	1	1	1	2	0	0	1	1	1	1
Thelaira americana	0	0	0	1	1	3	1	0	1	1	1	1
Thelaira nigripes	0	0	0	1	1	3	1	0	1	1	1	1
Thelairodes vittigera	1	0	0	1	1	7	0	0	1	1	1	0
Torocca munda	0	0	0	1	1	1	1	0	1	1	1	1
Torocca fasciata	0	0	0	1	1	1	1	0	1	1	1	1
Xanthodexia sericea	0	0	0	1	1	5	0	0	1	1	1	0
Halydaia luteicornis	0	0	0	1	1	1	1	0	1	1	1	0
Polygastropteryx bicoloripes	-	-	-	1	1	-	-	-	-	-	-	-
Eulasiona comstocki	?	?	?	1	1	?	?	?	?	?	?	?
Kirbya moerens	?	?	?	1	1	?	?	?	?	?	?	?
Aldrichiopa coracella	3	1	0	1	1	2	0	0	1	1	1	1
Rhamphina pedemontana	0	0	0	1	1	0	0	0	1	1	1	1
Stomina tachinoides	0	0	2	1	1	0	0	0	1	1	1	1
Doleschalla elongata	0	0	2	1	1	0	0	0	1	1	1	1
Doleschalla consobrina	0	0	2	1	1	0	0	0	1	1	1	1
Campylocheta lipernis	3	1	0	1	1	8	0	0	1	1	1	0
Campylocheta praecox	3	1	0	1	1	8	0	0	1	1	1	0
Campylocheta townsendi	3	1	0	1	1	8	0	0	1	1	1	0
Parahypochaeta genalis	3	1	0	1	1	8	0	0	1	1	1	0
Phyllomya volvulus	0	0	1	1	1	2	0	0	1	1	1	0
Leptothelaira longicauda	?	?	?	1	1	?	0	0	1	1	1	0
Cyrtophleba nigripalpis	3	1	0	1	1	1	4	0	1	1	1	1
Plagiomima spinolusa	?	?	?	1	1	?	?	?	?	?	?	?
Arrhinactia cylindrica	3	1	0	1	1	1	0	0	1	1	1	0
Athrycia cinerea	3	1	1	1	1	0	4	0	1	1	1	1
Cyrtophleba sp	3	1	0	1	1	0	0	0	1	1	1	0
Cyrtophleba ruricola	3	1	0	1	1	0	0	0	1	1	1	0

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Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Goniochaeta plagioides	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	0	0	0	-	0	0	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0
Hypovoria cauta	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	2	1	0	1	0	2	-	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	0
Minthoplagia rafaeli	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	1	0	0	2	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0
Paedarium sp	0	0	0	0	0	1	1	1	0	0	0	1	0	1	2	2	1	0	1	0	2	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0
Periscepsia helymus	0	0	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1	0	0	0
Periscepsia Ramonda	0	0	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	2	0	0	0	1	1	0	1	0	0	0
Periscepsia sp	0	0	0	0	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	2	0	0	0	1	1	0	1	0	0	0
Prosopochaeta nitidiventris	1	0	0	0	0	1	1	0	0	0	0	1	0	0	-	0	0	0	0	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0
Trichodischia soror	1	0	1	0	0	1	1	0	0	0	0	1	0	1	-	0	0	0	0	0	1	-	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Voria aurescens	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0
Voria ruralis	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	2	1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0
Alpinoplagia boliviana	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0
Ateloglutus chilensis	0	0	0	0	0	1	1	0	0	1	0	1	0	0	-	4	3	0	0	0	2	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0
Ateloglutus ruficornis	0	0	0	0	0	1	1	0	0	1	0	1	0	0	-	4	3	0	0	0	2	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0
Eriothrix rufomaculata	1	0	1	0	0	1	1	0	0	0	0	0	0	1	-	0	0	0	0	0	0	-	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0
Dexiomimops sp	1	0	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	0
Trafoia sp	1	0	1	0	2	1	1	0	0	0	0	1	0	0	-	0	0	0	1	0	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0
Blepharomyia pagana	0	0	0	0	0	1	1	0	0	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Euthera barbiellini	1	0	0	0	0	1	0	0	1	0	0	1	0	0	-	0	0	0	0	1	1	-	0	0	2	0	1	0	0	1	0	1	0	0	1	1	1	0	2	0
Euthera tuckeri	1	0	0	0	0	1	0	0	1	0	0	1	0	0	-	0	0	0	0	1	1	-	0	0	2	0	1	0	0	1	0	1	0	0	1	1	1	0	2	0
Beskia aelops	0	1	0	0	0	1	1	0	0	0	0	0	0	1	-	-	-	0	1	0	0	-	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	2	0
Epigrimyia illinoensis	0	0	0	0	0	1	1	0	0	0	0	0	0	1	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	2	0
Cordyligaster petiolatus	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Cordyligaster tipuliformis	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Euanthoides petiolata	1	0	0	0	3	0	1	0	1	0	0	0	0	0	-	5	-	0	0	0	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Neoeuantha aucta	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	1	0	0	0
Neosophia elongata	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	2
Telothyria itaquaquecetubae	1	0	0	0	3	1	1	0	0	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0
Telothyria rufostriata	1	0	0	0	3	1	1	0	0	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0
Uramya fasciata	1	0	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0
Uramya halisidotae	1	0	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0
Uramya longa	1	0	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0
Uramya producta	1	0	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0
Thelairaporia brasiliensis	1	0	1	0	0	1	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0
Trichodura anceps	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0

(continued)

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Goniochaeta plagioides	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0
Hypovoria cauta	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0
Minthoplagia rafaeli	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	1	1
Paedarium sp	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	2	-	0	0	0	0	0	0	0	0	0	1	1	2	1	0
Periscepsia helymus	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	1	0	1	-	1	0	0	0	0	0	0	0	0	1	1	1	1	0
Periscepsia Ramonda	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	0	0	1	1	2	1	0
Periscepsia sp	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	1	1	1	-	1	0	0	0	0	0	0	0	0	1	1	1	1	0
Prosopochaeta nitidiventris	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	2	-	0	0	0	0	0	2	0	0	0	1	1	1	0	0
Trichodischia soror	1	1	0	1	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Voria aurescens	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Voria ruralis	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Alpinoplagia boliviana	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	2	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Ateloglutus chilensis	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	2	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	2	1	0
Ateloglutus ruficornis	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	2	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	2	1	0
Eriothrix rufomaculata	1	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Dexiomimops sp	1	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Trafoia sp	1	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Blepharomyia pagana	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	?	?	?	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Euthera barbiellini	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	1	0	1	0	-	0	0
Euthera tuckeri	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	2	1	-	1	0	0	0	0	0	0	1	0	1	0	-	0	0
Beskia aelops	0	1	1	-	-	-	2	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	3	0	0	0	1	1	1	0	0
Epigrimyia illinoensis	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	3	0	0	0	1	1	0	0	0
Cordyligaster petiolatus	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	1	-	0	0	0	1	1	0	0	0	0	1	1	1	1	0
Cordyligaster tipuliformis	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0
Euanthoides petiolata	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	4	4	-	1	0	1	0	0	0	0	0	0	1	0	0	0	0
Neoeuantha aucta	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	2	4	-	1	0	1	0	0	0	0	0	0	1	1	0	0	0
Neosophia elongata	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	3	4	-	1	0	2	0	1	0	0	0	0	0	1	0	0	0
Telothyria itaquaquecetubae	0	1	0	1	0	1	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Telothyria rufostriata	0	1	0	1	0	1	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Uramya fasciata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Uramya halisidotae	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Uramya longa	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Uramya producta	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Thelairaporia brasiliensis	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Trichodura anceps	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0

(continued)

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Goniochaeta plagioides	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Hypovoria cauta	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	0
Minthoplagia rafaeli	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	2	2	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	0
Paedarium sp	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	1	0	0	2	0	1	0	1	1	0	1	0	2	0	0
Periscepsia helymus	3	0	0	1	0	0	0	0	0	4	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	2	0	1	0	1	1	0	1	0	2	0	0
Periscepsia Ramonda	3	0	0	1	0	0	0	0	0	4	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	2	0	1	0	1	1	0	1	0	2	0	0
Periscepsia sp	3	0	0	1	0	0	0	0	0	4	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	2	0	1	0	1	1	0	1	0	2	0	0
Prosopochaeta nitidiventris	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Trichodischia soror	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	1
Voria aurescens	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	-	-	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Voria ruralis	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	-	-	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Alpinoplagia boliviana	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Ateloglutus chilensis	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Ateloglutus ruficornis	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	3	0	0	2	0	1	0	1	1	0	1	0	2	0	1
Eriothrix rufomaculata	2	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Dexiomimops sp	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Trafoia sp	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1
Blepharomyia pagana	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Euthera barbiellini	3	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	1	0	0	0	1
Euthera tuckeri	3	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	1	0	0	0	1
Beskia aelops	1	1	0	1	1	0	0	0	0	1	3	0	0	0	0	0	0	4	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	2	0	1	1	0	0	0
Epigrimyia illinoensis	1	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	4	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Cordyligaster petiolatus	0	1	0	1	1	0	0	0	0	2	3	0	0	0	0	1	1	3	0	0	0	0	2	-	-	0	0	0	4	0	-	0	1	1	0	1	0	1	0	1
Cordyligaster tipuliformis	0	1	0	1	1	0	0	0	0	2	3	0	0	0	0	0	1	3	0	0	0	0	2	-	-	0	0	0	4	0	-	0	1	1	0	1	0	1	0	1
Euanthoides petiolata	2	1	0	1	1	0	0	0	0	3	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1
Neoeuantha aucta	0	1	0	1	1	0	0	0	0	3	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	1	0	1	0	1
Neosophia elongata	0	1	0	1	1	1	0	0	0	3	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	1
Telothyria itaquaquecetubae	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1
Telothyria rufostriata	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1
Uramya fasciata	0	1	0	1	1	0	0	0	0	1	2	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Uramya halisidotae	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Uramya longa	0	1	0	1	1	0	0	0	0	1	2	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Uramya producta	0	1	0	1	1	0	0	0	0	1	2	0	0	2	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Thelairaporia brasiliensis	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Trichodura anceps	0	1	0	1	1	0	0	0	0	1	2	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1

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Species	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Goniochaeta plagioides	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	5	-	1	0	0	0	0	0	0	4	-	1	0	0	1	0	0	0	0	0
Hypovoria cauta	0	0	0	0	0	1	0	0	1	0	0	1	2	1	0	0	0	0	1	0	5	-	1	0	0	0	0	0	0	4	-	1	0	0	1	0	0	0	0	0
Minthoplagia rafaeli	0	0	0	0	0	1	0	0	1	0	0	1	2	3	0	0	1	0	1	0	3	-	1	0	0	1	0	0	0	4	-	1	0	0	1	0	0	0	0	0
Paedarium sp	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	5	-	1	0	0	0	0	0	0	4	-	1	0	0	1	1	0	0	0	0
Periscepsia helymus	0	0	0	1	0	1	0	0	1	0	0	2	2	0	0	0	1	0	0	0	5	-	1	0	0	0	0	0	0	1	-	1	0	0	1	0	0	0	0	0
Periscepsia Ramonda	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4	-	1	0	0	0	0	0	0	1	-	1	0	0	1	4	0	0	0	0
Periscepsia sp	0	0	0	1	0	1	0	1	1	0	0	2	2	0	0	0	0	0	2	0	5	-	1	0	0	0	0	0	0	1	-	1	0	0	1	4	0	0	0	0
Prosopochaeta nitidiventris	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	-	0	0	0	0	1	0	0	1	2	1	0	0	1	0	0	0	0	0
Trichodischia soror	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	-	0	0	0	0	1	0	0	1	2	1	0	0	1	0	0	0	0	0
Voria aurescens	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	5	-	1	0	0	1	0	0	0	4	-	1	0	0	1	2	0	0	0	0
Voria ruralis	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	5	-	1	0	0	1	0	0	0	4	-	1	0	0	1	2	0	0	0	0
Alpinoplagia boliviana	0	0	0	0	0	1	1	0	1	0	0	1	2	3	0	0	0	0	1	0	3	-	1	0	0	1	0	0	0	4	-	1	0	0	1	2	0	0	0	0
Ateloglutus chilensis	0	0	0	0	0	1	0	0	1	0	0	1	2	3	0	0	1	0	1	0	3	-	1	0	0	0	0	0	0	4	-	1	0	0	1	1	0	0	0	0
Ateloglutus ruficornis	0	0	0	0	0	1	0	0	1	0	0	1	2	3	0	0	1	0	1	0	3	-	1	0	0	0	0	0	0	4	-	1	0	0	1	1	0	0	0	0
Eriothrix rufomaculata	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Dexiomimops sp	0	0	0	1	0	1	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	-	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Trafoia sp	0	0	0	0	0	1	0	0	0	0	0	0	2	2	1	0	0	0	1	1	0	-	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Blepharomyia pagana	0	0	0	0	0	1	0	0	0	0	0	0	2	2	1	0	0	0	1	0	0	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Euthera barbiellini	0	0	0	0	1	0	0	4	1	1	0	0	2	1	0	2	1	1	0	0	3	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	1	0	0
Euthera tuckeri	0	0	0	0	1	0	0	4	1	1	1	0	2	1	0	2	1	1	0	0	3	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	1	0	0
Beskia aelops	0	0	0	1	0	1	0	0	1	0	0	3	2	1	0	0	0	0	1	0	3	-	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1
Epigrimyia illinoensis	0	0	0	1	0	1	0	0	1	0	0	3	2	2	0	0	0	0	1	0	3	-	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1
Cordyligaster petiolatus	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0	2	0	0	5	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Cordyligaster tipuliformis	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0	2	0	0	5	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Euanthoides petiolata	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	2	0	1	0	0	0	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Neoeuantha aucta	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	2	0	1	0	0	3	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Neosophia elongata	0	0	0	1	0	1	0	0	0	0	0	0	1	2	0	2	0	0	0	0	3	-	0	0	0	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0
Telothyria itaquaquecetubae	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	1	2	1	0	0	1	0	0	0	0	0
Telothyria rufostriata	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	1	2	1	0	0	1	0	0	0	0	0
Uramya fasciata	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	3	-	1	0	0	1	0	0	0	0	0
Uramya halisidotae	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	3	-	1	0	0	1	0	0	0	0	0
Uramya longa	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	3	-	1	0	0	1	0	0	0	0	0
Uramya producta	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	3	-	1	0	0	1	0	0	0	0	0
Thelairaporia brasiliensis	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	2	0	0	0	0	0	-	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Trichodura anceps	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0

(continued)

Species	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Goniochaeta plagioides	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	?	?	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Hypovoria cauta	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Minthoplagia rafaeli	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	0	1	2	2	0	1	0	0	0	0	0	0	-
Paedarium sp	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	3	0	0	0	0	-
Periscepsia helymus	0	0	0	0	0	0	1	2	-	0	3	2	1	3	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Periscepsia Ramonda	0	0	0	0	0	0	1	2	-	0	3	2	1	3	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Periscepsia sp	0	0	0	0	0	0	1	2	-	0	3	2	1	3	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	0	0	0	0	0	-
Prosopochaeta nitidiventris	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trichodischia soror	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	1	0	3	-	-	-	-	-	1	1	2	1	0	1	2	0	1	0	0	0	-
Voria aurescens	0	0	0	0	0	1	1	2	-	0	6	1	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Voria ruralis	0	0	0	0	0	1	1	2	-	0	6	1	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Alpinoplagia boliviana	0	0	0	0	0	1	1	2	-	0	6	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Ateloglutus chilensis	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	?	?	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Ateloglutus ruficornis	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	?	?	0	0	3	-	-	-	-	-	1	1	2	2	0	1	0	0	0	0	0	0	-
Eriothrix rufomaculata	1	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	0	0	0	4	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Dexiomimops sp	0	0	0	0	0	1	0	2	-	0	0	1	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Trafoia sp	0	0	0	0	1	-	-	-	-	0	6	1	1	0	0	1	1	0	3	0	0	3	-	-	-	-	-	1	1	0	1	0	1	2	0	0	0	0	2	-
Blepharomyia pagana	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	3	-	-	-	-	-	1	1	0	1	0	1	2	0	0	0	0	0	-
Euthera barbiellini	0	0	0	1	1	-	-	-	-	0	4	1	1	0	0	1	0	0	2	1	2	3	-	-	-	-	-	1	0	1	1	0	1	0	0	0	0	0	0	-
Euthera tuckeri	0	0	0	1	1	-	-	-	-	0	4	1	1	0	0	1	0	0	2	1	2	3	-	-	-	-	-	1	0	1	1	0	1	0	0	0	0	0	0	-
Beskia aelops	0	0	0	0	0	1	0	0	?	0	7	1	1	0	0	1	0	0	2	0	0	6	-	-	-	-	-	1	1	2	1	0	1	0	0	0	0	0	0	-
Epigrimyia illinoensis	0	0	0	0	0	1	0	0	?	0	7	1	1	0	0	1	0	0	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cordyligaster petiolatus	1	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	0	0	0	1	0	1	0	0	0	0	-
Cordyligaster tipuliformis	1	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	1	1	0	0	0	1	0	1	0	0	0	0	-
Euanthoides petiolata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neoeuantha aucta	0	0	0	0	1	-	-	-	-	0	0	0	0	0	0	1	0	0	1	0	0	3	-	-	-	-	-	0	0	1	1	0	0	0	0	0	1	0	3	-
Neosophia elongata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	5	?	?	?	?	?	?	0	1	1	0	1	0	0	0	0	0	1	0
Telothyria itaquaquecetubae	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	1	0	0	1	0	-
Telothyria rufostriata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	1	0	0	1	0	-
Uramya fasciata	1	0	0	1	0	-	1	0	0	0	2	0	1	0	0	0	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Uramya halisidotae	1	0	0	1	0	-	1	0	0	0	2	0	1	0	0	0	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Uramya longa	1	0	0	1	0	-	1	0	0	0	2	0	1	0	0	0	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Uramya producta	1	0	0	1	0	-	1	0	0	0	2	0	1	0	0	0	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Thelairaporia brasiliensis	1	0	0	0	0	-	1	0	0	0	2	0	1	0	0	0	0	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Trichodura anceps	0	0	0	0	0	1	0	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	0	-

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Species	201	202	203	204	205	206	207	208	209	210	211	212
Goniochaeta plagioides	3	1	0	1	1	1	0	0	1	1	1	1
Hypovoria cauta	?	?	?	1	1	?	?	?	?	?	?	?
Minthoplagia rafaeli	3	1	0	1	1	8	4	0	1	1	1	1
Paedarium sp	3	1	0	1	1	0	0	0	1	1	1	0
Periscepsia helymus	3	1	0	1	1	8	0	0	1	1	1	0
Periscepsia Ramonda	3	1	0	1	1	8	0	0	1	1	1	0
Periscepsia sp	3	1	0	1	1	8	0	0	1	1	1	0
Prosopochaeta nitidiventris	?	?	?	1	1	?	?	?	?	?	?	?
Trichodischia soror	0	0	1	1	1	5	0	0	0	0	1	1
Voria aurescens	3	1	0	1	1	8	4	0	1	1	1	1
Voria ruralis	3	1	0	1	1	8	4	0	1	1	1	1
Alpinoplagia boliviana	3	1	0	1	1	8	4	0	1	1	1	1
Ateloglutus chilensis	3	1	1	1	1	8	4	0	1	1	1	1
Ateloglutus ruficornis	3	1	1	1	1	8	4	0	1	1	1	1
Eriothrix rufomaculata	0	0	1	1	1	0	1	0	1	1	1	1
Dexiomimops sp	0	0	1	1	1	?	1	0	1	1	1	1
Trafoia sp	0	0	1	1	1	5	0	0	1	0	1	1
Blepharomyia pagana	0	0	1	1	1	?	?	?	?	?	?	?
Euthera barbiellini	0	0	1	1	1	1	0	0	1	1	1	0
Euthera tuckeri	0	0	1	1	1	1	0	0	1	1	1	0
Beskia aelops	2	0	1	1	1	0	0	0	1	1	1	0
Epigrimyia illinoensis	?	?	?	1	1	?	?	?	?	?	?	?
Cordyligaster petiolatus	0	0	1	1	1	1	0	0	1	1	1	0
Cordyligaster tipuliformis	0	0	1	1	1	1	0	0	1	1	1	0
Euanthoides petiolata	?	?	?	1	1	?	?	?	?	?	?	?
Neoeuantha aucta	0	0	1	1	1	1	1	0	1	1	0	0
Neosophia elongata	0	0	1	1	1	1	0	0	1	1	1	1
Telothyria itaquaquecetubae	0	0	1	1	1	1	1	0	1	1	1	1
Telothyria rufostriata	0	0	1	1	1	1	1	0	1	1	1	0
Uramya fasciata	0	0	0	1	1	6	0	0	1	0	1	0
Uramya halisidotae	0	0	0	1	1	6	0	0	1	0	1	0
Uramya longa	0	0	0	1	1	6	0	0	1	0	1	0
Uramya producta	0	0	0	1	1	6	0	0	1	0	1	0
Thelairaporia brasiliensis	0	0	1	1	1	6	0	0	1	0	1	0
Trichodura anceps	0	0	1	1	1	2	1	0	1	1	1	0

(continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Trichodura lineata	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Trichodura vidua	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Trixa caerulescens	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	2	1	0	0	1	0	-	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Trixodes obesus	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	1	-	0	0	0	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	1	0	0
Diaugia angusta	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Neozelia alini	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	1	0	-	0	0	0	1	1	0	1	3	1	1	2	0	0	0	0	0	0	0
Ophirodexia pulchra	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Taperamyia sp	1	0	0	0	0	0	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Ushpayacua ureophila	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Yahuarmayoia phaeoptera	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Zelia lateralis	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0	0
Zelia plumosa	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Zelia potens	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0	0
Zelia vertebrata	1	0	0	0	0	0	1	0	1	0	0	0	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0	0
Rhamphinina sp	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	1	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Eudexia lopesi sp. nov.	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Hystrichodexia echinata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Microchaetina petiolata	1	0	0	0	0	1	1	0	0	1	0	0	0	0	-	0	0	0	0	2	1	-	0	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0	1	0
Mochlosoma lacertosum	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	1	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Myiomima sarcophagina	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Neomyostoma ptilodexioides	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Platyrrhinodexia punctulata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Prosenoides curvirostris	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Prosenoides flavipes	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Prosenoides haustellata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Ptilodexia conjuncta	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Ptilodexia pacifica	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Ptilodexia sp Brazil	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Sarcocalirrhoe trivittata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Scotiptera sp	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Scotiptera venatoria	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Tropidopsiomorpha tropica	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Billaea claripalpis	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Billaea lata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	1	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Billaea menezi	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0

(continued)

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Trichodura lineata	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0
Trichodura vidua	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0
Trixa caerulescens	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	2	0	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Trixodes obesus	0	0	0	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Diaugia angusta	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Neozelia alini	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Ophirodexia pulchra	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Taperamyia sp	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Ushpayacua ureophila	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Yahuarmayoia phaeoptera	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Zelia lateralis	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Zelia plumosa	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Zelia potens	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	1	0	0	0	1	1	1	0	0
Zelia vertebrata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Rhamphinina sp	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Eudexia lopesi sp. nov.	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	1	-	0	0	0	0	0	4	0	0	0	1	1	0	0	0
Hystrichodexia echinata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	4	0	0	0	1	1	0	0	0
Microchaetina petiolata	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Mochlosoma lacertosum	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Myiomima sarcophagina	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Neomyostoma ptilodexioides	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Platyrrhinodexia punctulata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Prosenoides curvirostris	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Prosenoides flavipes	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Prosenoides haustellata	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Ptilodexia conjuncta	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Ptilodexia pacifica	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Ptilodexia sp Brazil	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Sarcocalirrhoe trivittata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Scotiptera sp	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Scotiptera venatoria	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Tropidopsiomorpha tropica	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	4	0	0	0	1	1	0	0	0
Billaea claripalpis	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Billaea lata	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Billaea menezi	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0

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Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Trichodura lineata	0	1	0	1	1	0	0	0	0	1	2	0	0	2	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Trichodura vidua	0	1	0	1	1	0	0	0	0	1	2	0	0	2	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Trixa caerulescens	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Trixodes obesus	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
Diaugia angusta	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Neozelia alini	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Ophirodexia pulchra	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Taperamyia sp	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Ushpayacua ureophila	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Yahuarmayoia phaeoptera	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Zelia lateralis	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Zelia plumosa	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Zelia potens	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Zelia vertebrata	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Rhamphinina sp	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Eudexia lopesi sp. nov.	0	1	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Hystrichodexia echinata	0	1	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Microchaetina petiolata	3	0	0	0	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Mochlosoma lacertosum	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Myiomima sarcophagina	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Neomyostoma ptilodexioides	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Platyrrhinodexia punctulata	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
Prosenoides curvirostris	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1
Prosenoides flavipes	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1
Prosenoides haustellata	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1
Ptilodexia conjuncta	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Ptilodexia pacifica	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Ptilodexia sp Brazil	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Sarcocalirrhoe trivittata	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Scotiptera sp	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Scotiptera venatoria	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Tropidopsiomorpha tropica	0	1	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Billaea claripalpis	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Billaea lata	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Billaea menezi	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1

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Species	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Trichodura lineata	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Trichodura vidua	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Trixa caerulescens	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Trixodes obesus	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Diaugia angusta	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Neozelia alini	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Ophirodexia pulchra	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Taperamyia sp	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Ushpayacua ureophila	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Yahuarmayoia phaeoptera	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Zelia lateralis	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Zelia plumosa	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Zelia potens	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Zelia vertebrata	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Rhamphinina sp	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Eudexia lopesi sp. nov.	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Hystrichodexia echinata	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Microchaetina petiolata	0	0	0	1	1	0	1	0	1	1	0	0	2	1	2	2	1	1	3	0	5	-	0	0	0	0	2	0	0	3	-	0	0	0	1	4	0	0	0	0
Mochlosoma lacertosum	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Myiomima sarcophagina	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Neomyostoma ptilodexioides	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Platyrrhinodexia punctulata	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Prosenoides curvirostris	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Prosenoides flavipes	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Prosenoides haustellata	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Ptilodexia conjuncta	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Ptilodexia pacifica	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Ptilodexia sp Brazil	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Sarcocalirrhoe trivittata	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Scotiptera sp	0	0	0	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Scotiptera venatoria	0	0	0	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Tropidopsiomorpha tropica	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Billaea claripalpis	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Billaea lata	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Billaea menezi	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0

(continued)

Species	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Trichodura lineata	0	0	0	0	0	1	0	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Trichodura vidua	0	0	0	0	0	1	0	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Trixa caerulescens	0	0	0	1	0	1	0	2	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	0
Trixodes obesus	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	2	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Diaugia angusta	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	?	?	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Neozelia alini	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Ophirodexia pulchra	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Taperamyia sp	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0
Ushpayacua ureophila	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0
Yahuarmayoia phaeoptera	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0
Zelia lateralis	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Zelia plumosa	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Zelia potens	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Zelia vertebrata	0	0	0	0	0	1	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-
Rhamphinina sp	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	1	1	-	-	1	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Eudexia lopesi sp. nov.	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	-
Hystrichodexia echinata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	1	0	1	0	0	1	0	0	0	0	0	0	-
Microchaetina petiolata	0	0	0	0	0	3	-	2	-	0	0	0	0	0	0	1	0	0	2	0	0	1	0	0	2	2	0	0	0	1	0	0	0	0	0	0	0	0	1	1
Mochlosoma lacertosum	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	-
Myiomima sarcophagina	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	2	0	1	0	1	0	0	1	0	1	0	0	0	0	-
Neomyostoma ptilodexioides	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Platyrrhinodexia punctulata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Prosenoides curvirostris	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	2
Prosenoides flavipes	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	2
Prosenoides haustellata	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	2
Ptilodexia conjuncta	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Ptilodexia pacifica	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Ptilodexia sp Brazil	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Sarcocalirrhoe trivittata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	2	0	1	0	1	0	0	1	0	1	0	0	0	0	-
Scotiptera sp	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	1	-	-	0	0	1	0	1	0	0	1	0	1	0	0	0	0	-
Scotiptera venatoria	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	1	-	-	0	0	1	0	1	0	0	1	0	1	0	0	0	0	-
Tropidopsiomorpha tropica	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	-
Billaea claripalpis	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Billaea lata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	2
Billaea menezi	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	0

(continued)

Species	201	202	203	204	205	206	207	208	209	210	211	212
Trichodura lineata	0	0	1	1	1	2	1	0	1	1	1	0
Trichodura vidua	0	0	1	1	1	2	1	0	1	1	1	0
Trixa caerulescens	0	0	1	1	1	2	1	0	1	1	1	0
Trixodes obesus	0	0	2	1	1	0	1	0	1	1	1	0
Diaugia angusta	0	0	2	1	1	2	1	0	1	1	1	0
Neozelia alini	0	0	2	1	1	2	1	0	1	1	1	0
Ophirodexia pulchra	0	0	2	1	1	2	1	0	1	1	1	0
Taperamyia sp	0	0	2	1	1	2	1	0	1	1	1	0
Ushpayacua ureophila	0	0	2	1	1	2	1	0	1	1	1	0
Yahuarmayoia phaeoptera	0	0	2	1	1	2	1	0	1	1	1	0
Zelia lateralis	0	0	2	1	1	2	1	0	1	1	1	0
Zelia plumosa	0	0	2	1	1	2	1	0	1	1	1	0
Zelia potens	0	0	2	1	1	2	1	0	1	1	1	0
Zelia vertebrata	0	0	2	1	1	2	1	0	1	1	1	0
Rhamphinina sp	0	0	1	1	1	1	1	0	1	1	1	0
Eudexia lopesi sp. nov.	0	0	0	1	1	2	1	0	1	1	1	0
Hystrichodexia echinata	0	0	0	1	1	2	1	0	1	1	1	0
Microchaetina petiolata	0	0	0	1	1	0	0	0	1	1	0	0
Mochlosoma lacertosum	0	0	1	1	1	2	1	0	1	1	1	0
Myiomima sarcophagina	0	0	1	1	1	5	1	0	1	1	1	0
Neomyostoma ptilodexioides	0	0	1	1	1	1	1	0	1	1	1	0
Platyrrhinodexia punctulata	0	0	1	1	1	2	1	0	1	1	1	0
Prosenoides curvirostris	0	0	2	1	1	2	1	0	1	1	1	0
Prosenoides flavipes	0	0	2	1	1	2	1	0	1	1	1	0
Prosenoides haustellata	0	0	2	1	1	2	1	0	1	1	1	0
Ptilodexia conjuncta	0	0	1	1	1	1	1	0	1	1	1	0
Ptilodexia pacifica	0	0	1	1	1	1	1	0	1	1	1	0
Ptilodexia sp Brazil	0	0	1	1	1	1	1	0	1	1	1	0
Sarcocalirrhoe trivittata	0	0	0	1	1	5	1	0	1	1	1	0
Scotiptera sp	0	0	0	1	1	4	0	0	1	1	1	0
Scotiptera venatoria	0	0	0	1	1	4	0	0	1	1	1	0
Tropidopsiomorpha tropica	0	0	0	1	1	2	1	0	1	1	1	0
Billaea claripalpis	0	0	2	1	1	2	1	0	1	1	1	0
Billaea lata	0	0	2	1	1	2	1	0	1	1	1	0
Billaea menezi	0	0	2	1	1	2	1	0	1	1	1	0

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Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Billaea rhynchophorae	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Billaea rutilans	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Billaea minor	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	2	1	0	0	2	1	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Chaetogyne analis	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Chaetogyne vexans	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Chaetotheresia crassa	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Ateloglossa marginalis	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	2	1	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Daetaleus purpureus	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	1	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0
Dasyuromyia inornata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	1	0	-	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0
Dexia fulvifera	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Dexia rhodesia	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Dexia rustica	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Dexia uelensis	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Dexia vacua	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Dexia varivittata	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	1	0	-	0	0	2	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Dinera ferina	1	0	0	0	0	1	1	0	1	1	0	0	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Dinera grisescens	1	0	0	0	0	1	1	0	1	1	0	0	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Estheria bohemani	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	2	1	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Estheria cristata	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	2	1	0	0	2	1	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Estheria picta	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	1	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Philippodexia longipes	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	?	0	0	0	2	0	-	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Geraldia nuda	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	1	1	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Morphodexia barrosi	0	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	1	-	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0
Pelycops darwini	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Prophorostoma pulchra	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Prosena siberita	1	0	0	0	0	1	1	0	1	1	0	0	0	0	-	0	0	0	0	1	0	-	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Prosenina sandemani	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Heterometopia argentea	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	2	1	1	0	3	0	-	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0
Psecacera chiliensis	0	0	0	0	0	1	1	0	1	1	0	1	0	0	-	3	0	0	0	0	1	-	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0
Pseudodexia eques	1	0	0	0	0	1	1	0	0	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0
Rasiliverpa agrianomei	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	0	-	0	0	1	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0
Rutilotrixa nigrithorax	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	0	1	2	1	-	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0
Senostoma longipes	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	3	0	0	0	2	1	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Chrysopasta elegans	1	0	0	0	0	1	1	0	1	1	0	1	0	0	-	0	0	0	0	2	1	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Formosia heinronthi	1	0	0	0	0	0	1	0	1	0	0	1	0	0	-	3	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0

(continued)

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Billaea rhynchophorae	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Billaea rutilans	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Billaea minor	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Chaetogyne analis	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Chaetogyne vexans	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Chaetotheresia crassa	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Ateloglossa marginalis	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Daetaleus purpureus	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Dasyuromyia inornata	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Dexia fulvifera	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Dexia rhodesia	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Dexia rustica	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Dexia uelensis	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Dexia vacua	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Dexia varivittata	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Dinera ferina	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Dinera grisescens	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Estheria bohemani	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Estheria cristata	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Estheria picta	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Philippodexia longipes	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Geraldia nuda	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Morphodexia barrosi	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Pelycops darwini	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	0	0	1	0	1	1	-	1	1	0	0	0	0	0	0	0	1	1	0	0	0
Prophorostoma pulchra	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Prosena siberita	0	1	0	0	1	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Prosenina sandemani	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Heterometopia argentea	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Psecacera chiliensis	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Pseudodexia eques	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	2	0	0	0	0	1	0	0	0
Rasiliverpa agrianomei	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Rutilotrixa nigrithorax	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Senostoma longipes	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Chrysopasta elegans	0	1	0	1	0	1	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	-	0	0	0	0	0	0	1	0	0	1	1	0	0	0
Formosia heinronthi	0	1	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	3	0	0	0	1	0	3	1	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0

(continued)

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Billaea rhynchophorae	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Billaea rutilans	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Billaea minor	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Chaetogyne analis	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Chaetogyne vexans	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Chaetotheresia crassa	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Ateloglossa marginalis	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Daetaleus purpureus	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dasyuromyia inornata	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1
Dexia fulvifera	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dexia rhodesia	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dexia rustica	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dexia uelensis	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dexia vacua	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dexia varivittata	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dinera ferina	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Dinera grisescens	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Estheria bohemani	2	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Estheria cristata	2	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Estheria picta	2	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Philippodexia longipes	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Geraldia nuda	2	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Morphodexia barrosi	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1
Pelycops darwini	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1
Prophorostoma pulchra	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Prosena siberita	0	1	0	1	1	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	2	0	1	0	1
Prosenina sandemani	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
Heterometopia argentea	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1
Psecacera chiliensis	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1
Pseudodexia eques	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	2	0	1	1
Rasiliverpa agrianomei	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1
Rutilotrixa nigrithorax	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Senostoma longipes	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
Chrysopasta elegans	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Formosia heinronthi	0	1	1	1	1	0	0	1	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	1	0	1

(continued)

Species	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Billaea rhynchophorae	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Billaea rutilans	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Billaea minor	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Chaetogyne analis	0	0	0	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Chaetogyne vexans	0	0	0	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Chaetotheresia crassa	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Ateloglossa marginalis	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Daetaleus purpureus	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Dasyuromyia inornata	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	2	1	0	0	1	0	0	0	0	0
Dexia fulvifera	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Dexia rhodesia	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Dexia rustica	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Dexia uelensis	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Dexia vacua	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Dexia varivittata	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Dinera ferina	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Dinera grisescens	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Estheria bohemani	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	1	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Estheria cristata	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	1	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Estheria picta	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	1	0	0	1	0	1	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Philippodexia longipes	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Geraldia nuda	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Morphodexia barrosi	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Pelycops darwini	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Prophorostoma pulchra	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Prosena siberita	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0
Prosenina sandemani	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Heterometopia argentea	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Psecacera chiliensis	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	2	1	0	0	1	0	0	0	0	0
Pseudodexia eques	0	0	0	0	1	0	0	0	1	0	0	0	2	2	0	0	0	3	1	0	1	2	0	0	0	0	2	0	0	3	-	1	0	0	1	4	0	0	1	0
Rasiliverpa agrianomei	0	0	0	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	1	3	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Rutilotrixa nigrithorax	0	0	0	0	0	1	0	0	0	?	0	0	2	1	0	1	0	0	1	0	1	3	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Senostoma longipes	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
Chrysopasta elegans	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Formosia heinronthi	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0

(continued)

Species	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Billaea rhynchophorae	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Billaea rutilans	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	2
Billaea minor	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	1	2
Chaetogyne analis	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	1
Chaetogyne vexans	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	1
Chaetotheresia crassa	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	2	1	1	0	1	0	0	1	0	0	0	0	0	1	0
Ateloglossa marginalis	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Daetaleus purpureus	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	2	1	1	0	1	0	0	1	0	1	0	0	0	0	-
Dasyuromyia inornata	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	2	1	0	1	0	1	0	0	1	0	0	0	0	0	0	-
Dexia fulvifera	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Dexia rhodesia	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Dexia rustica	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Dexia uelensis	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Dexia vacua	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	2	1	4	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Dexia varivittata	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	1	0
Dinera ferina	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Dinera grisescens	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Estheria bohemani	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Estheria cristata	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	3	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Estheria picta	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	3	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Philippodexia longipes	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	3	-	-	-	-	-	0	0	1	0	0	1	0	1	0	0	0	0	-
Geraldia nuda	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	?	?	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Morphodexia barrosi	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	2	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0
Pelycops darwini	0	1	0	1	1	-	-	-	-	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Prophorostoma pulchra	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	1	-	-	1	0	1	0	1	0	0	1	0	0	0	0	0	0	-
Prosena siberita	0	0	0	0	0	1	0	2	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	3	1	3	0	0	0	1	0	0	1	0	0	0	0	0	1	1
Prosenina sandemani	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	0	-
Heterometopia argentea	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	2	0	1	4	0	1	0	1	0	0	1	0	4	0	0	0	0	-
Psecacera chiliensis	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	2	2	1	1	0	1	0	0	1	0	0	0	0	0	0	-
Pseudodexia eques	0	0	0	2	1	-	-	-	-	0	0	0	0	0	0	1	0	0	1	0	0	3	-	-	-	-	-	1	0	0	2	0	1	0	2	0	0	0	0	-
Rasiliverpa agrianomei	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	?	?	?	?	?	?	?	0	1	0	0	1	?	?	?	?	?	?	?
Rutilotrixa nigrithorax	0	0	0	0	0	3	1	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	2	2	0	1	0	1	0	0	1	0	0	0	0	0	2	0
Senostoma longipes	0	0	0	1	0	1	0	2	-	0	0	0	1	0	0	1	0	0	2	0	0	1	0	0	2	2	0	1	0	1	0	0	1	0	0	0	0	0	2	1
Chrysopasta elegans	0	0	0	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	1	-	-	1	1	0	0	1	0	1	1	0	0	0	0	1	1	2
Formosia heinronthi	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	2	3	0	2	1	1	1	0	1	0	1	1	0	0	0	0	0	1	3

(continued)

Species	201	202	203	204	205	206	207	208	209	210	211	212
Billaea rhynchophorae	0	0	2	1	1	2	1	0	1	1	1	0
Billaea rutilans	0	0	2	1	1	2	1	0	1	1	1	0
Billaea minor	0	0	2	1	1	2	1	0	1	1	1	0
Chaetogyne analis	0	0	1	1	1	2	1	0	1	1	1	0
Chaetogyne vexans	0	0	1	1	1	2	1	0	1	1	1	0
Chaetotheresia crassa	0	0	0	1	1	5	?	?	?	1	1	0
Ateloglossa marginalis	0	0	1	1	1	2	1	0	1	1	1	0
Daetaleus purpureus	0	0	2	1	1	2	0	0	1	1	1	0
Dasyuromyia inornata	0	0	2	1	1	2	1	0	1	1	1	0
Dexia fulvifera	0	0	2	1	1	2	1	0	1	1	1	0
Dexia rhodesia	0	0	2	1	1	2	1	0	1	1	1	0
Dexia rustica	0	0	2	1	1	2	1	0	1	1	1	0
Dexia uelensis	0	0	2	1	1	2	1	0	1	1	1	0
Dexia vacua	0	0	2	1	1	2	1	0	1	1	1	0
Dexia varivittata	0	0	2	1	1	2	1	0	1	1	1	0
Dinera ferina	0	0	0	1	1	2	1	0	1	1	1	0
Dinera grisescens	0	0	0	1	1	2	1	0	1	1	1	0
Estheria bohemani	0	0	0	1	1	2	1	0	1	1	1	0
Estheria cristata	0	0	0	1	1	2	1	0	1	1	1	0
Estheria picta	0	0	0	1	1	2	1	0	1	1	1	0
Philippodexia longipes	0	0	1	1	1	2	1	0	1	1	1	0
Geraldia nuda	0	0	0	1	1	2	1	0	1	1	1	0
Morphodexia barrosi	0	0	0	1	1	2	1	0	1	1	1	0
Pelycops darwini	0	0	0	1	1	2	1	0	1	1	1	0
Prophorostoma pulchra	0	0	0	1	1	5	1	0	1	1	1	0
Prosena siberita	0	0	1	1	1	2	1	0	1	1	1	0
Prosenina sandemani	0	0	1	1	1	2	1	0	1	1	1	0
Heterometopia argentea	0	0	2	1	1	2	1	0	1	1	1	0
Psecacera chiliensis	0	0	1	1	1	2	1	0	1	1	1	0
Pseudodexia eques	0	2	1	1	1	0	4	0	1	1	2	0
Rasiliverpa agrianomei	?	0	?	1	1	0	1	0	1	1	1	0
Rutilotrixa nigrithorax	0	0	1	1	1	0	1	0	1	1	1	0
Senostoma longipes	0	0	0	1	1	0	1	0	1	1	1	0
Chrysopasta elegans	0	0	1	1	1	0	3	0	1	1	1	0
Formosia heinronthi	0	0	1	1	1	0	3	0	1	1	1	0

(continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Formosia solomonicola	1	0	0	0	0	0	1	0	1	0	0	1	0	0	-	3	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Prodiaphania victoriae	1	0	0	0	0	0	1	0	1	0	0	1	0	0	-	3	0	0	0	2	0	-	0	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Rutilia albovirida	1	0	0	0	0	0	1	0	1	0	0	1	0	0	-	3	0	0	1	2	1	-	1	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Rutilia caeruleata	1	0	0	0	0	0	1	0	1	0	0	1	0	0	-	3	0	0	1	2	1	-	1	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Rutilia setosa	1	0	0	0	0	0	1	0	1	0	0	1	0	0	-	3	0	0	1	2	1	-	1	0	2	0	1	0	0	1	1	1	2	0	0	0	0	0	1	0
Phasia sp	1	0	0	0	0	1	0	1	1	0	0	1	0	0	-	5	-	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	0
Eutrichopoda pyrrhogaster	1	0	0	0	0	1	0	0	1	0	0	1	0	0	-	5	-	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	0
Leucostoma aterrimum	1	0	0	0	1	1	1	0	0	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0
Irengia sp	1	0	0	0	0	1	1	0	0	0	0	1	0	1	-	0	0	0	0	0	0	-	0	1	0	0	1	0	1	1	1	1	2	0	0	0	1	0	1	2
Uruleskia aurescens	1	0	0	0	0	1	1	0	0	0	0	0	0	0	-	0	0	0	0	2	0	-	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0
Winthemia pinguis	1	0	1	0	0	1	1	0	0	1	0	1	0	1	-	0	0	0	1	0	1	-	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0
Lespesia lata	1	0	1	0	0	1	1	0	0	1	0	1	0	0	-	0	0	0	1	0	1	-	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	1
Archytas incertus	0	0	0	0	0	1	1	0	0	1	0	1	1	1	-	1	1	0	0	2	1	-	0	0	0	0	1	0	0	1	0	1	0	0	2	1	1	0	1	0
Eutrixa sp	1	0	0	0	3	1	0	0	0	1	0	1	0	0	-	5	-	1	0	0	1	-	0	1	0	0	1	0	1	1	1	1	0	0	0	0	1	0	1	0
Palpostoma pallens	1	0	0	0	3	1	0	0	0	1	0	1	0	0	-	2	1	0	0	0	1	-	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0
Chetoptilia puella	1	0	0	0	0	1	0	0	0	0	0	1	0	0	-	0	0	1	0	0	0	-	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0
Dufouria chalybeata	1	0	1	0	0	1	1	0	0	1	0	1	0	0	-	0	0	0	0	1	0	-	0	0	0	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0
Oestrophasia calva	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	1	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0
Euoestrophasia plaumanni	1	0	0	0	0	1	1	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0
Microsoma exiguum	1	0	0	0	0	1	1	1	1	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0
Freraea gagatea	1	0	0	0	0	0	1	1	1	0	0	1	0	0	-	5	-	0	0	0	1	3	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	1	-	0
Imitomyia sugens	0	0	0	0	0	1	1	0	1	0	0	1	0	0	-	5	-	0	0	0	0	-	0	0	2	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0
Cholomyia inaequipes	1	0	0	0	0	1	1	0	1	0	0	1	0	0	-	0	0	1	0	0	1	-	0	0	0	0	1	0	1	1	1	1	2	0	0	0	1	0	0	0

(continued)

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Formosia solomonicola	0	1	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	3	0	0	0	1	0	3	1	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Prodiaphania victoriae	0	1	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	3	0	0	0	1	0	1	1	-	0	0	0	0	0	0	1	0	0	1	1	0	0	0
Rutilia albovirida	0	1	0	1	0	1	1	0	1	1	0	0	1	0	1	0	0	3	0	0	0	1	0	3	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Rutilia caeruleata	0	1	0	1	0	1	1	0	1	1	0	0	1	0	1	0	0	3	0	0	0	1	0	3	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Rutilia setosa	0	1	0	1	0	1	1	0	1	1	0	0	1	0	1	0	0	3	0	0	0	1	0	3	1	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Phasia sp	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	3	1	-	1	0	0	0	0	4	0	0	0	1	1	0	0	0
Eutrichopoda pyrrhogaster	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	-	1	0	0	0	0	2	0	0	0	1	1	0	0	0
Leucostoma aterrimum	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Irengia sp	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Uruleskia aurescens	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Winthemia pinguis	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0
Lespesia lata	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Archytas incertus	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	3	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Eutrixa sp	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	2	1	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0
Palpostoma pallens	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	2	0	0	0	0	1	1	1	0	0
Chetoptilia puella	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	2	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Dufouria chalybeata	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	2	2	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Oestrophasia calva	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Euoestrophasia plaumanni	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Microsoma exiguum	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	2	2	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Freraea gagatea	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	0	1	1	1	3	2	0	1	0	0	0	0	0	0	0	0	1	0	3	0	0
Imitomyia sugens	0	1	0	1	0	1	2	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	0	3	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Cholomyia inaequipes	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0

(continued)

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Formosia solomonicola	0	1	1	1	1	0	0	1	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Prodiaphania victoriae	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Rutilia albovirida	0	1	1	1	1	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Rutilia caeruleata	0	1	1	1	1	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Rutilia setosa	0	1	1	1	1	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Phasia sp	3	1	1	1	1	0	1	-	0	1	2	0	0	0	0	0	0	4	0	3	3	2	1	3	0	0	0	1	1	0	0	0	1	1	0	4	0	0	0	1
Eutrichopoda pyrrhogaster	2	1	1	1	1	0	1	-	0	1	1	1	0	0	0	0	0	4	0	3	3	2	1	3	0	0	0	1	1	0	0	0	1	2	0	4	0	0	0	1
Leucostoma aterrimum	2	1	1	1	1	0	0	0	0	1	3	0	0	0	0	1	0	4	0	3	3	2	1	3	0	0	0	1	1	0	0	0	1	1	0	4	0	0	0	0
Irengia sp	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	1
Uruleskia aurescens	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Winthemia pinguis	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
Lespesia lata	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
Archytas incertus	0	1	1	1	1	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	2	0	2	2	0	5	0	0	1	0	2	0	3	0	0	0	1
Eutrixa sp	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	1	0	0	0	0
Palpostoma pallens	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	3	0	0	1	0	0	0	0	0	0	1	0	0	1	2	0	1	0	0	0	0
Chetoptilia puella	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	4	0	0	1	2	1	2	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	2
Dufouria chalybeata	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	0	2
Oestrophasia calva	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	4	0	4	0	2	0	3	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	2
Euoestrophasia plaumanni	0	1	0	1	1	0	0	0	0	1	3	0	0	0	0	1	0	4	0	4	0	2	1	3	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	2
Microsoma exiguum	2	1	0	1	1	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	2
Freraea gagatea	0	1	0	1	1	0	1	-	0	1	3	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	1	0	0	1	1	0	1	0	0	0	2
Imitomyia sugens	3	1	0	1	1	0	1	-	0	1	2	1	0	0	0	0	0	0	0	3	3	0	1	3	0	0	0	0	0	-	0	0	1	1	0	4	0	0	0	0
Cholomyia inaequipes	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0

(continued)

Species	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Formosia solomonicola	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Prodiaphania victoriae	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Rutilia albovirida	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Rutilia caeruleata	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Rutilia setosa	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Phasia sp	1	0	1	1	2	0	1	3	1	0	0	5	2	1	4	3	1	-	2	0	5	-	1	2	1	0	2	1	0	5	-	0	0	0	0	5	1	0	0	0
Eutrichopoda pyrrhogaster	1	0	1	1	2	0	1	3	1	0	0	5	2	1	4	3	1	-	2	0	5	-	1	2	1	0	2	1	0	5	-	0	0	0	0	5	1	0	0	0
Leucostoma aterrimum	1	0	1	1	2	0	1	3	1	0	1	3	2	1	0	3	1	2	2	0	5	-	1	2	1	0	2	1	0	5	-	0	0	0	0	5	1	0	0	5
Irengia sp	0	0	0	4	1	0	1	0	1	0	1	4	2	1	0	0	3	3	1	0	5	-	0	0	0	0	2	0	0	6	-	1	0	0	1	6	0	0	0	0
Uruleskia aurescens	0	0	0	0	1	0	0	4	1	0	0	4	2	1	1	0	3	2	0	0	5	-	0	0	0	0	2	0	0	6	-	1	0	0	1	4	0	0	0	0
Winthemia pinguis	0	0	0	2	1	0	0	4	1	0	0	4	2	1	0	0	3	0	0	0	3	-	0	0	0	0	2	0	0	6	-	0	0	0	1	4	0	0	0	2
Lespesia lata	0	0	0	1	1	0	0	4	1	0	1	4	2	1	0	0	3	0	0	0	3	-	0	0	0	0	2	0	0	6	-	0	0	0	1	4	0	0	0	0
Archytas incertus	0	0	0	4	1	0	0	2	1	0	0	4	2	1	3	0	3	1	0	0	0	-	0	0	0	0	2	0	0	5	-	1	0	1	0	6	0	0	0	0
Eutrixa sp	0	0	0	1	0	1	1	0	1	0	1	0	2	1	1	0	0	0	0	0	0	-	0	0	0	0	2	0	0	1	2	1	0	0	1	3	0	0	0	3
Palpostoma pallens	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0	2	?	0	5	-	0	0	0	0	2	0	0	1	2	0	0	0	1	0	0	0	0	0
Chetoptilia puella	0	0	0	0	0	1	1	0	0	0	0	0	3	2	5	0	1	0	0	0	5	-	0	0	0	2	2	1	0	2	2	1	1	0	1	7	0	0	0	0
Dufouria chalybeata	0	0	0	1	0	1	1	0	0	0	0	0	3	2	5	0	1	0	0	0	5	-	0	0	0	2	2	1	0	2	2	1	1	0	1	7	0	0	0	0
Oestrophasia calva	0	0	0	1	0	1	1	0	0	0	0	0	3	2	5	0	1	0	0	0	5	-	0	0	0	2	2	1	0	2	2	1	1	0	1	7	0	0	0	1
Euoestrophasia plaumanni	0	0	0	1	0	1	1	0	0	0	0	0	3	2	5	0	1	0	0	0	5	-	0	0	0	2	2	1	0	2	2	1	1	0	1	7	0	0	0	1
Microsoma exiguum	0	0	0	1	0	1	0	0	0	0	0	0	3	2	0	0	1	0	0	0	5	-	0	1	0	0	2	0	0	2	2	1	0	0	1	3	0	0	0	0
Freraea gagatea	0	0	0	1	0	1	0	0	0	0	0	0	3	2	0	0	1	0	0	0	5	-	0	0	0	0	1	0	0	2	2	1	0	0	1	4	0	0	0	3
Imitomyia sugens	1	0	0	1	0	0	1	0	1	0	0	0	2	1	2	0	1	0	3	0	3	-	0	0	1	0	2	0	0	5	-	1	0	0	2	1	0	1	0	2
Cholomyia inaequipes	0	0	0	1	1	0	0	0	1	0	1	4	0	1	0	0	0	2	0	0	3	-	0	0	0	0	2	0	0	6	-	1	0	0	1	4	0	0	0	0

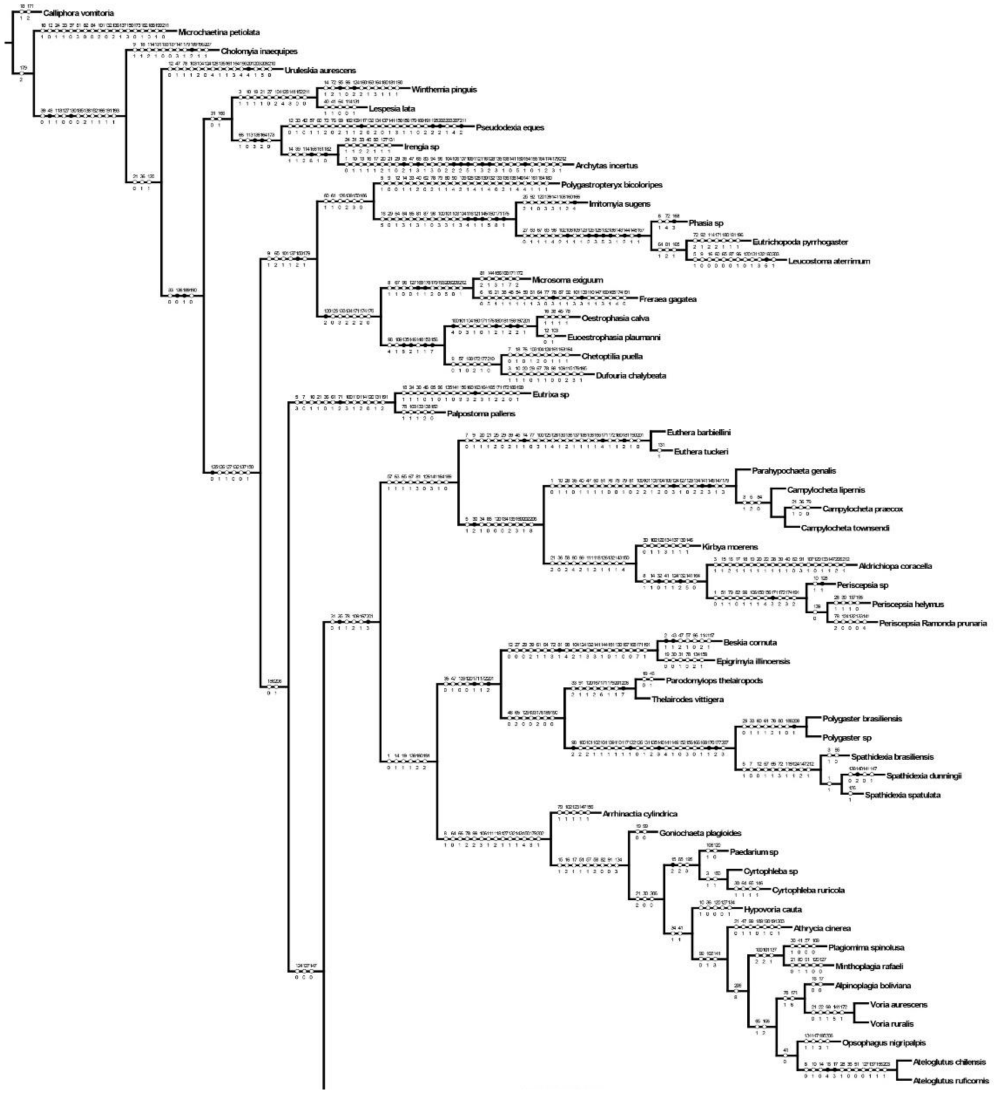
(continued)

Species	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Formosia solomonicola	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	2	3	0	1	1	1	1	0	1	0	1	1	0	0	0	0	0	1	3
Prodiaphania victoriae	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	2	3	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0	1	3
Rutilia albovirida	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	2	4	0	2	1	0	0	0	1	0	1	1	0	0	0	0	0	1	2
Rutilia caeruleata	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	2	4	0	2	1	0	0	0	1	0	1	1	0	0	0	0	0	1	2
Rutilia setosa	0	0	0	0	1	-	-	-	-	0	0	0	1	0	0	1	0	0	2	0	0	2	4	0	2	1	0	0	0	1	0	1	1	0	0	0	0	0	1	2
Phasia sp	0	0	0	0	0	0	0	3	-	0	8	2	1	4	1	-	-	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Eutrichopoda pyrrhogaster	0	0	0	0	1	-	-	-	-	0	2	0	1	4	1	-	-	0	1	1	1	3	-	-	-	-	-	1	1	0	1	0	1	0	0	1	0	0	0	-
Leucostoma aterrimum	0	0	0	0	1	-	-	-	-	0	8	2	1	4	1	-	-	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Irengia sp	1	0	0	2	1	-	-	-	-	0	0	0	0	0	0	1	0	0	2	0	0	0	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Uruleskia aurescens	1	0	0	3	0	1	0	2	-	0	0	0	1	0	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	1	1	0	1	0	4	0	0	0	0	-
Winthemia pinguis	0	0	1	3	1	-	-	-	-	0	0	0	1	1	0	1	0	0	2	1	1	3	-	-	-	-	-	1	1	1	1	0	1	0	0	0	0	0	0	-
Lespesia lata	0	0	0	0	1	-	-	-	-	0	0	0	1	2	0	1	0	0	2	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Archytas incertus	1	0	0	1	1	-	-	-	-	0	0	0	0	2	0	1	0	0	3	0	0	0	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Eutrixa sp	0	0	2	3	1	-	-	-	-	0	2	2	1	0	0	1	0	0	2	0	0	3	-	-	-	-	-	1	0	1	2	0	1	0	0	0	0	0	0	-
Palpostoma pallens	0	0	0	0	0	1	0	2	-	0	0	0	1	0	0	1	0	0	2	0	?	3	-	-	-	-	-	1	1	0	2	0	1	0	0	0	0	0	0	-
Chetoptilia puella	1	0	1	1	0	-	0	0	0	0	2	2	1	2	0	0	1	0	1	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	0	0	0	0	0	-
Dufouria chalybeata	0	0	0	0	0	-	0	0	0	0	2	2	1	2	0	0	1	0	3	0	0	3	-	-	-	-	-	1	1	0	1	0	1	0	1	0	0	0	0	-
Oestrophasia calva	0	0	0	0	0	1	0	2	-	0	0	0	1	2	0	1	0	0	1	2	1	3	-	-	-	-	-	1	1	0	1	0	2	0	0	0	2	-	-	-
Euoestrophasia plaumanni	0	0	0	0	0	1	0	2	-	0	0	0	1	2	0	1	0	0	1	2	1	3	-	-	-	-	-	1	1	0	1	0	2	0	0	0	2	-	-	-
Microsoma exiguum	0	0	0	0	0	-	0	1	1	0	7	2	1	2	0	0	0	1	2	0	0	3	-	-	-	-	-	1	1	0	1	0	0	0	0	0	0	0	0	-
Freraea gagatea	0	0	0	0	1	-	-	-	-	0	2	0	1	4	0	0	0	1	2	0	0	3	-	-	-	-	-	1	1	0	0	0	0	0	0	0	0	0	0	-
Imitomyia sugens	0	0	0	0	0	4	0	2	-	0	8	1	1	3	1	-	-	0	1	0	0	3	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Cholomyia inaequipes	0	0	0	0	0	1	0	2	-	0	0	0	1	0	0	1	0	0	1	0	0	3	-	-	-	-	-	1	2	-	1	0	1	0	1	0	0	0	0	-

(continued)

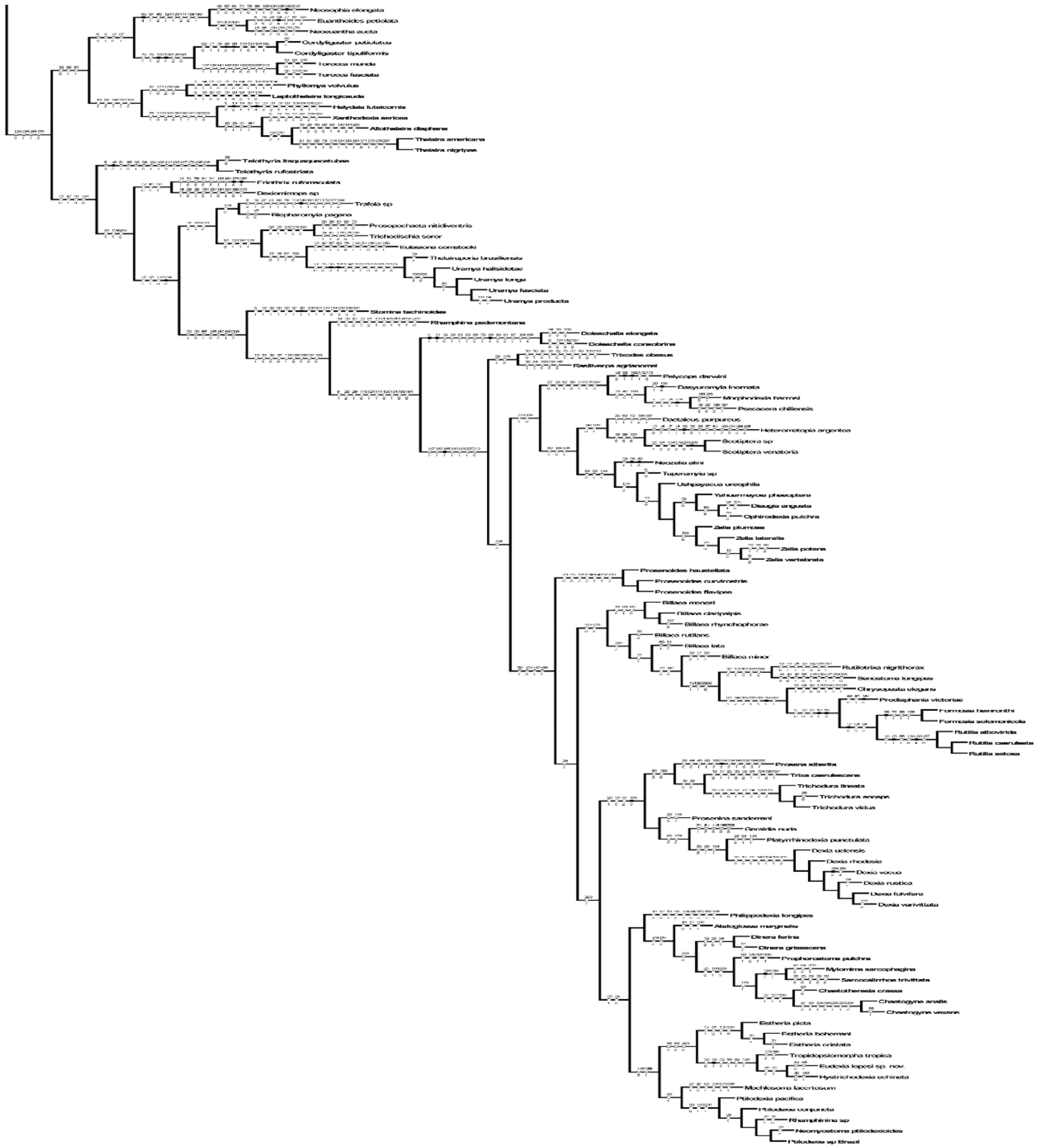
Species	201	202	203	204	205	206	207	208	209	210	211	212
Formosia solomonicola	0	0	1	1	1	0	3	0	1	1	1	0
Prodiaphania victoriae	0	0	1	1	1	0	3	0	1	1	1	0
Rutilia albovirida	0	0	1	1	1	0	3	0	1	1	1	0
Rutilia caeruleata	0	0	1	1	1	0	3	0	1	1	1	0
Rutilia setosa	0	0	1	1	1	0	3	0	1	1	1	0
Phasia sp	0	0	0	1	1	0	0	0	1	1	1	0
Eutrichopoda pyrrhogaster	0	0	0	1	1	0	1	0	1	1	1	0
Leucostoma aterrimum	0	0	1	1	1	0	1	0	1	1	1	0
Irengia sp	0	0	0	1	1	0	0	0	1	1	1	0
Uruleskia aurescens	4	0	1	1	1	5	0	0	1	0	1	0
Winthemia pinguis	0	0	0	1	1	0	0	0	1	1	0	0
Lespesia lata	0	0	0	1	1	0	0	0	1	1	0	0
Archytas incertus	0	0	0	1	1	0	0	0	1	1	1	1
Eutrixa sp	0	0	1	1	1	1	0	0	1	1	1	0
Palpostoma pallens	0	0	0	1	1	1	0	0	1	1	1	0
Chetoptilia puella	0	0	0	1	1	1	1	0	1	0	1	0
Dufouria chalybeata	0	0	0	1	1	8	1	0	1	0	1	0
Oestrophasia calva	1	0	0	1	1	0	1	0	1	1	1	0
Euoestrophasia plaumanni	1	0	0	1	1	0	1	0	1	1	1	0
Microsoma exiguum	0	0	0	1	1	5	1	0	0	1	1	1
Freraea gagatea	0	0	0	1	1	5	1	0	0	1	1	1
Imitomyia sugens	?	?	?	1	1	?	?	?	?	?	?	?
Cholomyia inaequipes	0	0	0	1	1	0	1	0	1	1	1	0

Appendix 3. Cladograms showing ACCTRAN, DELTRAN optimization the Bremer index

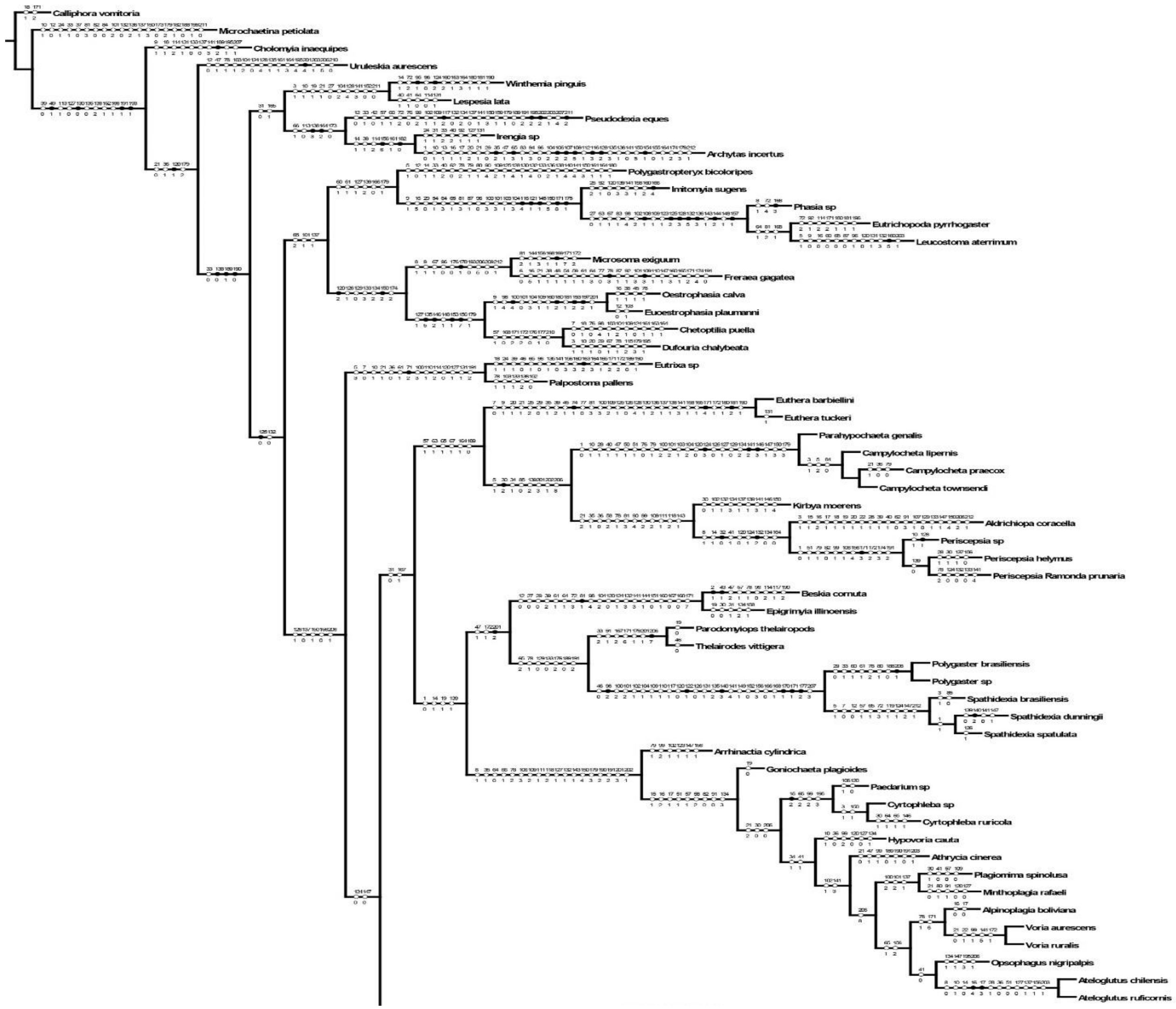


Most parsimonious cladogram resulting from the cladistic analysis with equal weighting analysis under ACCTRAN optimization.

(continued)



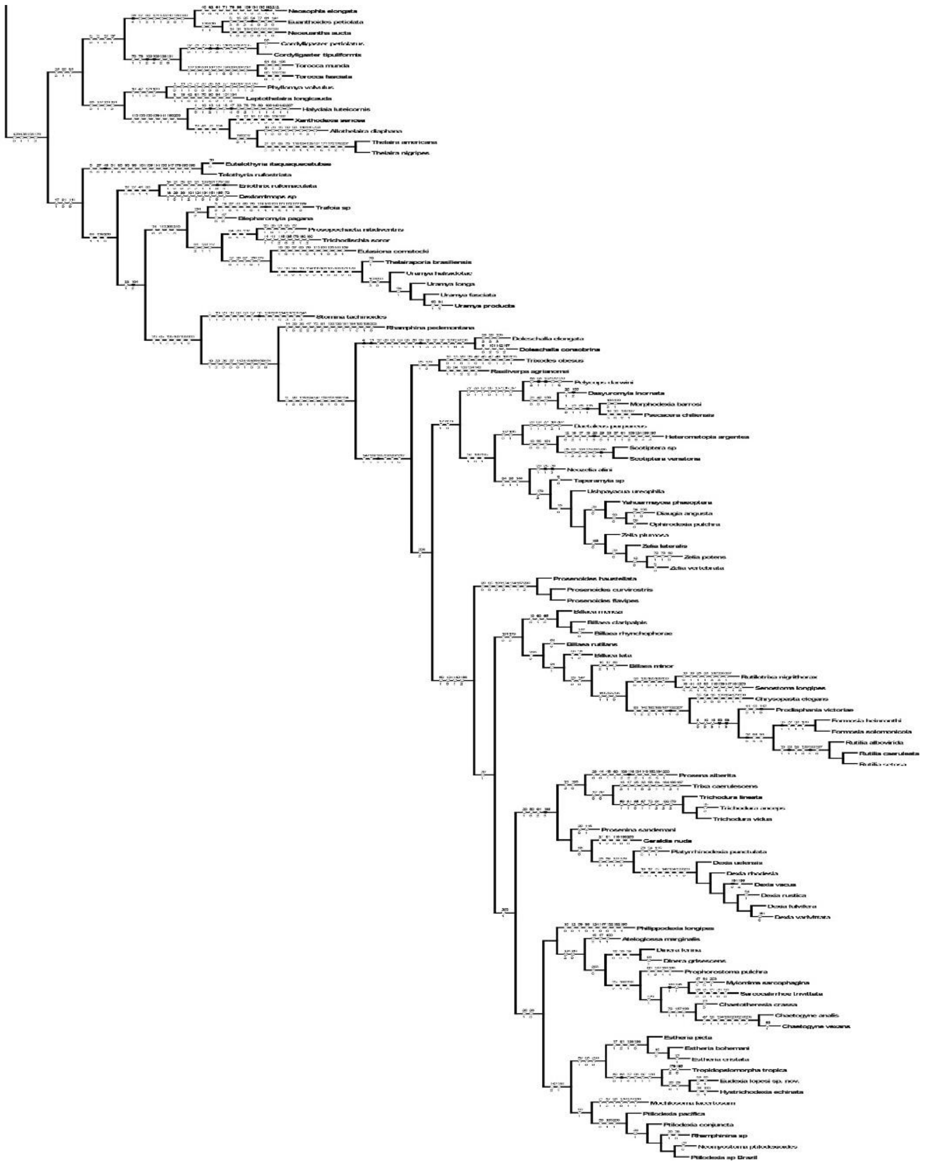
Continuation. Most parsimonious cladogram resulting from the cladistic analysis with equal weighting analysis under ACCTRAN optimization.



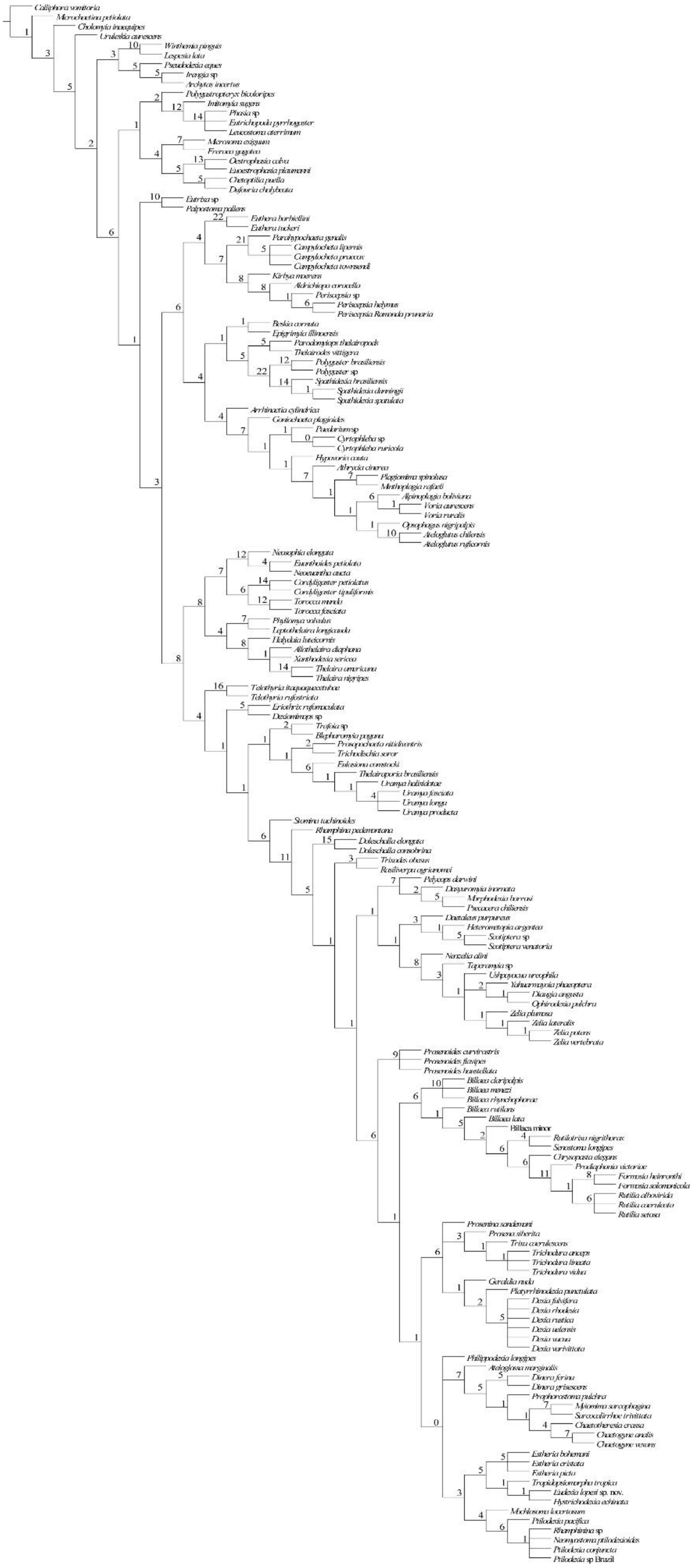
(continued)

Most parsimonious cladogram resulting from the cladistic analysis with equal weighting analysis under DELTRAN optimization.

(continued)



Continuation. Most parsimonious cladogram resulting from the cladistic analysis with equal weighting analysis under DELTRAN optimization.



Most parsimonious cladogram resulting from the cladistic analysis with equal weighting analysis, the numbers above the nodes represent the Bremer index (1994) of each clade.

Appendix 4. New classification scheme for the subfamilies Dexiinae and Dufouriinae.

Subfamily DEXIINAE Macquart, 1834

(13 tribes, 274 genera)

CAMPYLOCHETINI Townsend, 1936 - **Tribe revalidated**

Type genus: *Campylocheta* Rondani,1859.

Genera included: *Campylocheta* Rondani, 1859; *Elfriedella* Mesnil, 1957; *Homohypochaeta* Townsend, 1927; *Hypochaetopsis* Townsend, 1915; *Parahypochaeta* Brauer & Bergenstamm, 1891.

DEXIINI Macquart, 1834

Dexiariae Macquart, 1834. Type-genus: *Dexia* Meigen, 1826.

The following two tribes, that were valid before this work, are herein considered as **synonymous** with Dexiini:

(1) Doleschaliini Brauer & Bergenstamm, 1889: 80, 128 **syn. nov.** Type genus: *Doleschalla* Walker, 1861;

(2) Rutiliini Brauer & Bergenstamm, 1889: 76, 152 **syn. nov.** Type genus: *Rutilia* Robineau-Desvoidy, 1830;

The following two tribes, that were invalid before this work and placed in Voriini (O'Hara et al., 2020), are herein considered as **new synonymous** of Dexiini:

(3) Stominini Townsend, 1936 (*sensu* Mesnil, 1974) **syn. nov.** Type genus: *Stomina* Robineau-Desvoidy, 1830;

(4) Rhamphinini Mesnil, 1939 (*sensu* Mesnil, 1974) **syn. nov.** Type genus: *Rhamphina* Macquart, 1835

(Currently invalid tribes: Prosenini Townsend, 1892; Theresiini Townsend, 1919; Trichodurini Townsend, 1919; Trixodini Townsend, 1908; Zeliini Townsend, 1919)

Genera included: *Amphibolia* Macquart, 1843 (**new placement**); *Amphitropesa* Townsend, 1933; *Ateloglossa* Coquillett, 1899; *Bathydexia* Wulp, 1891; *Billaea* Robineau-Desvoidy, 1830; *Callotroxis* Aldrich, 1929; *Camarona* Wulp, 1891; *Cantrellius* Barraclough, 1992; *Chaetocalirrhoe* Townsend, 1935; *Chaetodexia* Mesnil, 1976; *Chaetogyne* Brauer & Bergenstamm, 1889; *Chaetotheresia* Townsend, 1931; *Charapozelia* Townsend, 1927; *Chetogaster* Macquart, 1851 (**new placement**); *Chrysopasta* Brauer & Bergenstamm, 1889 (**new placement**); *Cordillerodexia* Townsend, 1927; *Daetaleus* Aldrich, 1928; *Dasyuromyia* Bigot, 1885; *Dexia* Meigen, 1826; *Diaugia* Perty, 1833; *Dinera* Robineau-Desvoidy, 1830; *Doleschalla* Walker, 1861 (**new placement**); *Dolichocodia* Townsend, 1908; *Dolichodinera* Townsend, 1935; *Echinodexia* Brauer & Bergenstamm, 1893; *Effusimentum* Barraclough, 1992; *Estheria* Robineau-Desvoidy, 1830;

Euchaetogyne Townsend, 1908; *Eudexia* Brauer & Bergenstamm, 1889; *Eumegaparia* Townsend, 1908; *Eupododexia* Villeneuve, 1915; *Eutrixoides* Walton, 1913; *Exodexia* Townsend, 1927; *Formodexia* Crosskey, 1973 (**new placement**); *Formosia* Guerin-Meneville, 1843 (**new placement**); *Frontodexia* Mesnil, 1976; *Gemursa* Barraclough, 1992; *Geraldia* Malloch, 1930; *Gigamyiopsis* Reinhard, 1964; *Heterometopia* Macquart, 1846; *Huascarodexia* Townsend, 1919; *Hyadesimyia* Bigot, 1888; *Hyosoma* Aldrich, 1934; *Hystrichodexia* Roder, 1886; *Hystrysyphona* Bigot, 1859; *Jurinodexia* Townsend, 1915; *Leptodexia* Townsend, 1919; *Macrometopa* Brauer & Bergenstamm, 1889; *Mastigiomyia* Reinhard, 1964; *Megaparia* Wulp, 1891; *Megapariopsis* Townsend, 1915; *Mesnilotrix* Cerretti & O'Hara, 2016; *Microaporia* Townsend, 1919; *Microchaetogyne* Townsend, 1931; *Milada* Richter, 1973; *Mitannia* Herting, 1987; *Mochlosoma* Brauer & Bergenstamm, 1889; *Morphodexia* Townsend, 1931; *Myiodexia* Cortes & Campos, 1971; *Myiomima* Brauer & Bergenstamm, 1889; *Myioscotiptera* Giglio-Tos, 1893; *Neomyostoma* Townsend, 1935; *Neozelia* Guimaraes, 1975; *Nicephorus* Reinhard, 1944; *Nimioglossa* Reinhard, 1945; *Notodytes* Aldrich, 1934; *Oberonomyia* Reinhard, 1964; *Ochrocera* Townsend, 1916; *Ocyrtosoma* Townsend, 1912; *Ophirodexia* Townsend, 1911; *Opsotheresia* Townsend, 1919; *Orestilla* Reinhard, 1944; *Orthosimyia* Reinhard, 1944; *Pachymyia* Macquart, 1843; *Patulifrons* Barraclough, 1992; *Paulipalpus* Barraclough, 1992; *Pelycops* Aldrich, 1934; *Phalacrophyto* Townsend, 1915; *Phasiops* Coquillett, 1899; *Philippodexia* Townsend, 1926; *Piligena* Emden, 1947; *Piligenoides* Barraclough, 1985; *Pirionimyia* Townsend, 1931; *Platydexia* Emden, 1954; *Platyrrhinodexia* Townsend, 1927; *Platytainia* Macquart, 1851; *Pododexia* Brauer & Bergenstamm, 1889; *Pretoriamyia* Curran, 1927; *Prodiaphania* Townsend, 1927 (**new placement**); *Promegaparia* Townsend, 1931; *Prophorostoma* Townsend, 1927; *Prorhynchops* Brauer & Bergenstamm, 1891; *Prosena* Lepeletier & Serville, 1828; *Prosenina* Malloch, 1930; *Prosenoides* Brauer & Bergenstamm, 1891; *Psecacera* Bigot, 1880; *Pseudodexilla* O’Hara, Shima & Zhang, 2009; *Pseudodinera* Brauer & Bergenstamm, 1891; *Ptilodexia* Brauer & Bergenstamm, 1889; *Punamyocera* Townsend, 1919; *Rasiliverpa* Barraclough, 1992; *Rhamphina* Macquart, 1835 (**new placement**); *Rhamphinina* Bigot, 1885; *Rutilia* Robineau-Desvoidy, 1830 (**new placement**); *Rutilodexia* Townsend, 1915 (**new placement**); *Rutilotrixa* Townsend, 1933; *Sarcocalirrhoe* Townsend, 1928; *Sarcoprosena* Townsend, 1927; *Schistostephana* Townsend, 1919; *Scotiptera* Macquart, 1835; *Senostoma* Macquart, 1847; *Setolestes* Aldrich, 1934; *Sitellitergus* Reinhard, 1964; *Stomina* Robineau-Desvoidy, 1830 (**new placement**); *Sturmiodexia* Townsend, 1919; *Subfischeria* Villeneuve 1937 (**new placement**); *Sumichrastia* Townsend, 1916; *Taperamyia* Townsend, 1935; *Tesseracephalus* Reinhard, 1955; *Trichodura* Macquart, 1843; *Trichostylum* Macquart, 1851; *Trinitodexia* Townsend, 1935; *Trixa* Meigen, 1824; *Trixiceps* Villeneuve, 1936; *Trixodes* Coquillett, 1902; *Tromodesiopsis* Townsend, 1927; *Tropidodexia* Townsend, 1915; *Tropidopsiomorpha* Townsend, 1927; *Tylodexia* Townsend, 1926; *Tyreomma* Brauer & Bergenstamm, 1891; *Urodexiomima* Townsend, 1927; *Ursophyto* Aldrich, 1926; *Ushpayacua* Townsend, 1928; *Villanovia* Strobl, 1910; *Xanthotheresia* Townsend, 1931; *Yahuarmayoia* Townsend, 1927; *Zelia* Robineau-Desvoidy 1830; *Zeliomima* Mesnil, 1976; *Zeuxia* Meigen, 1826; *Zeuxiotrix* Mesnil, 1976.

EPIGRIMYIINI Townsend, 1908

Type genus: *Epigrimyia* Townsend, 1891.

Genera included: *Epigrimyia* Townsend, 1891; *Beskia* Brauer & Bergenstamm, 1889.

ERIOTRICHINI Townsend, 1913 - **Tribe revalidated**

Eriothrixini Townsend 1936 (incorrect spelling). Type genus: *Eriothrix* Meigen, 1803. (Included here the former subtribe Dexiomimopsina Mesnil, 1966).

Genera included: *Dexiomimops* Townsend, 1926; *Eriothrix* Meigen, 1803; *Feriola* Mesnil, 1957.

EUTHERINI Townsend, 1912

Type-genus: *Euthera* Loew, 1866.

Genera included: *Euthera* Loew, 1866; *Redtenbacheria* Schiner 1861.

PHYLLOMYINI Mesnil, 1939 - **Tribe revalidated**

Phyllomyina Mesnil, 1939. Type genus: *Phyllomya* Robineau-Desvoidy, 1830.

Genera included: *Engeddia* Kugler, 1977; *Leptothelaira* Mesnil & Shima, 1979; *Itamintho* Townsend, 1931; *Phyllomya* Robineau-Desvoidy, 1830.

SPATHIDEXIINI Townsend 1912b - **Tribe revalidated**

Type genus: *Spathidexia* Townsend, 1912.

Genera included: *Spathidexia* Townsend, 1912; *Parodomyiops* Townsend, 1935; *Polygaster* Wulp, 1890; *Thelairodes* Wulp, 1891.

SOPHIINI Townsend, 1936

Type-genus: *Sophia* Robineau-Desvoidy, 1830 (Included here the former subtribe Euanthina Mesnil, 1966).

Genera included: *Cordyligaster* Macquart, 1851; *Cryptosophia* Santis 2018; *Euantha* Wulp, 1891; *Euanthoides* Townsend, 1931; *Leptidosophia* Townsend 1931; *Neoeuantha* Townsend, 1931; *Neosophia* Guimarães, 1982; *Sophia* Robineau-Desvoidy, 1830; *Sophiella* Guimarães, 1982; *Torocca* Walker, 1859 (**new placement)**.

TELOTHYRIINI Townsend, 1927

Type genus: *Telothyria* van der Wulp, 1890.

Genus included: *Telothyria* van der Wulp, 1890

THELAIRINI, Lioy, 1864 - **Tribe revalidated**

Thelareini, Lioy, 1864. Type genus: *Thelaira* Robineau-Desvoidy, 1830.

Genera included: *Actinochaetopteryx* Townsend, 1927; *Allothelaira* Villeneuve, 1915; *Halydaia* Egger, 1856; *Nephochaetona* Townsend, 1919; *Prosheliomyia* Brauer & Bergenstamm, 1891; *Rhombothyria* Wulp, 1891; *Solomonilla* Ozdikmen, 2007; *Spiroglossa* Doleschall, 1858; *Thelaira* Robineau-Desvoidy, 1830; *Thryptodexia* Malloch, 1926; *Xanthodexia* Wulp, 1891; *Xanthopteromyia* Townsend, 1926; *Zambesa* Walker, 1856; *Zonalia* Curran, 1934.

URAMYINI Townsend, 1919

Type-genus: *Uramya* Robineau-Desvoidy, 1830 (Includes former subtribe Eulasionina Mesnil, 1966).

Genera included: *Blepharomyia* Brauer & Bergenstamm, 1889 (**new placement**); *Dischotrichia* Cortés, 1944 (**new placement**); *Eulasiona* Townsend, 1892 (**new placement**); *Itaplectops* Townsend, 1927; *Matucania* Townsend, 1919; *Metopomuscopteryx* Townsend, 1915 (**new placement**); *Muscopteryx* Townsend, 1892 (**new placement**); *Prosopochaeta* Macquart, 1851 (**new placement**); *Piriona* Aldrich, 1928 (**new placement**); *Thelairaporia* Guimarães, 1980; *Trafoia* Brauer & Bergenstamm, 1893 (**new placement**); *Trichodischia* Bigot, 1885 (**new placement**); *Trinitodexia* Townsend, 1935; *Uramya* Robineau-Desvoidy, 1830.

VORIINI Townsend, 1912

Type-genus: *Voria* Robineau-Desvoidy, 1830.

Genera included: *Aglummyia* Townsend, 1912 (**new placement**); *Aldrichomyia* Ozdikmen, 2006; *Alexogloblinia* Cortés, 1945; *Alpinoplagia* Townsend, 1931; *Argyromima* Brauer & Bergenstamm, 1889; *Arrhinactia* Townsend, 1927; *Ateloglutus* Aldrich, 1934; *Athrycia* Robineau-Desvoidy, 1830; *Bahrettinia* Ozdikmen, 2007; *Calcager* Hutton, 1901; *Calcageria* Curran, 1927; *Cesamorelosia* Kocak & Kemal, 2010; *Chaetodemoticus* Brauer & Bergenstamm, 1891; *Chaetonopsis* Townsend, 1915; *Chaetoplagia* Coquillett, 1895; *Chaetovoria* Villeneuve, 1920; *Chiloclista* Townsend, 1931; *Cockerelliana* Townsend, 1915; *Coracomyia* Aldrich, 1934; *Cowania* Reinhard, 1952; *Cyrtophleba* Rondani, 1856; *Doliolomyia* Reinhard, 1975; *Elfriedella* Mesnil, 1957; *Euptilopareia* Townsend, 1916; *Ganopleuron* Aldrich, 1934; *Goniochaeta* Townsend, 1891; *Haracca* Richter, 1995; *Heliaea* Curran, 1934; *Hyleorus* Aldrich, 1926; *Hypovoria* Villeneuve, 1913; *Klugia* Robineau-Desvoidy, 1863; *Leptomacquartia* Townsend, 1919; *Meledonus* Aldrich, 1926; *Meleterus* Aldrich, 1926; *Metaplagia* Coquillett, 1895; *Micronychiops* Townsend, 1915; *Microplagia* Townsend, 1915; *Minthoplagia* Townsend, 1915; *Myiochaeta* Cortes, 1967; *Myioclura* Reinhard, 1975; *Myiophasiopsis* Townsend, 1927; *Nanoplagia* Villeneuve, 1929; *Nardia* Cerretti, 2009; *Neochaetoplagia* Blanchard, 1963; *Neocyrtophoeba* Vimmer & Soukup, 1940; *Neopaedarium* Blanchard, 1943; *Neosolieria* Townsend, 1927; *Neotrafoiopsis* Townsend, 1931; *Nephoplagia* Townsend, 1919; *Nothovoria* Cortés & Gonzalez, 1989; *Opsophagus* Aldrich, 1926 **stat. rev.**; *Pachynocera* Townsend, 1919; *Paedarium* Aldrich, 1926; *Phaeodema* Aldrich, 1934; *Phasiophyto* Townsend, 1919; *Plagiomima* Brauer & Bergenstamm, 1891; *Plagiomyia* Curran, 1927; *Prosenactia* Blanchard, 1940; *Pseudorrhinactia* Thompson, 1968; *Reichardia* Karsch, 1886; *Squamomedina* Townsend, 1934; *Stenodexia* van der Wulp, 1891; *Trichopyrrhosia* Townsend, 1927; *Trismegistomya* Reinhard, 1967; *Trochilochaeta* Townsend, 1940; *Trochilodes* Coquillett, 1903; *Uclesia* Girschner, 1901; *Uclesiella* Malloch, 1938; *Velardemyia* Valencia, 1972; *Voria* Robineau-Desvoidy, 1830.

WAGNERIINI Mesnil, 1939 - **Tribe revalidated**

Wagneriina Mesnil, 1939. Type genus: *Wagneria* Robineau-Desvoidy, 1830.

Genera included: *Aldrichiopa* Guimarães, 1971; *Carbonilla* Mesnil, 1974; *Kirbya* Robineau-Desvoidy, 1830; *Periscepsia* Gistel, 1848; *Peteina* Meigen, 1838; *Wagneria* Robineau-Desvoidy 1830.

Unplaced genera of Dexiinae

Carmodymyia Thompson, 1968; *Euthyprosopiella* Blanchard, 1963; *Litophasia* Girschner, 1887; *Medinophyto* Townsend, 1927; *Melanesomyia* Barraclough, 1997; *Schlingermyia* Cortés, 1967.

Subfamily DUFOURIINAE Robineau-Desvoidy, 1830

(3 tribes, 13 genera)

DUFOURIINI Robineau-Desvoidy, 1830

Type genus: *Dufouria* Robineau-Desvoidy, 1830.

Genera included: *Chetoptilia* Rondani, 1862; *Comyops* Wulp, 1891; *Dufouria* Robineau-Desvoidy, 1830; *Ebenia* Macquart, 1846; *Rondania* Robineau-Desvoidy, 1850.

FRERAEINI Townsend, 1936

Type genus: *Freraea* Robineau-Desvoidy 1830.

Genera included: *Eugymnopeza* Townsend, 1933; *Freraea* Robineau-Desvoidy 1830; *Microsoma* Macquart 1855; *Pandelleia* Villeneuve, 1907.

OESTROPHASIINI Brauer & Bergenstamm, 1889

Type genus: *Oestrophasia* Brauer & Bergenstamm, 1889.

Genera included: *Cenosoma* Wulp, 1890; *Euoestrophasia* Townsend, 1892; *Jamacaria* Curran, 1928; *Oestrophasia* Brauer & Bergenstamm, 1889.

Unplaced genera of Tachinidae formerly in Dexiinae

Bolbocheta Bigot, 1885; *Ceratometopa* Townsend, 1931; *Tromodesiana* Townsend, 1931.

Appendix 5. Characters supporting the new classification scheme, including ACCTRAN and DELTRAN optimizations.

Clade 1

Included subfamilies: (Dexiinae (Phasiinae + Dufouriinae))

Autapomorphies: male terminalia with connection between basiphallus (dorsal sclerite) and distiphallus membranous (125: 0; fig. 9F). Additional apomorphic character states: male terminalia with distiphallus differenced in ventral, dorsal, and median ridge (132: 0; fig. 9F). In ACCTRAN, male terminalia with membranous connection between basiphallus (dorsal sclerite) and distiphallus, 180º movement capacity movable (126: 1; fig. 9F); basiphallus short in relation to postgonite; distiphallus with anterior portion of dorsal sclerite with equal width in relation ventral sclerite and pregonite platiform, with equal sclerotization (150: 1).

Clade 2

Included subfamilies: Phasiinae + Dufouriinae.

Autapomorphies: male terminalia with pregonite platiform, medially expanded (150: 2) in ACCTRAN. Additional apomorphic character states: anepimeron with setae slim and short (65: 2); male terminalia with tergite 6 about half the size in length to segment 7+8 (110: 1); first instar larva with cephaloskeleton presenting the mouth hook unciform (207: 1). In ACCTRAN, frontal setae ending before the base of antennae insertion (9: 1; fig. 4C); male terminalia with distiphallus with expanded anterior portion (137: 1); spermatheca with low roughness (179: 1).

Dufouriinae (clade 3)

Included tribes: Dufouriini, Freraeini and Oestrophasiini.

Autapomorphies: male terminalia with the boundary of the hypandrial apodeme in relation to central plate indistinct (120: 2) and the platiform pregonite medially expanded (150: 2), in DELTRAN. Additional apomorphic character states: male terminalia with basiphallus prolonged in relation to epiphallus (120: 0); distiphallus with extension of the dorsal sclerite more than a half of the median ridge length (133: 3); distiphallus with the extension of the dorsal sclerite shorter in length relative to pregonite (134: 2; fig. 9F) and female terminalia with sternite 10 narrow and shorter than tergite 7 (174: 2). In ACCTRAN, female terminalia with sternite 8 conical (171: 2); sternite 9 elongated (176: 0; fig. 11A). In DELTRAN, male terminalia with distiphallus, 180º movement capacity movable (126: 1; fig. 9F).

Dexiinae (clade 4)

Included tribes: Campylochetini, **tribe rev**.; Dexiini; Epigrimyiini; Eutherini; Thelairini, Spathidexiini, **tribe rev**; Wagneriini, **tribe rev**.; Sophiini; Phyllomyini, **tribe rev**.; Eriotrichini **tribe rev**.; Uramyini; Telothyriini; Voriini.

Autapomorphies: none. Additional apomorphic character states: male terminalia with postgonite with posterior region concave (as a crescent moon) (156: 0; fig. 10A) and first instar larva with sclerite of the salivary gland of the cephaloskeleton narrow anteriorly, wide posteriorly (206: 1; fig. 13A). In DELTRAN: male terminalia with membranous connection between basiphallus (dorsal sclerite) and distiphallus, 180º movement capacity movable (126: 1; fig. 9F); distiphallus, with anterior portion with the dorsal sclerite with equal width in relation ventral sclerite (137: 0) and pregonite platiform, with equal sclerotifization (150:1; fig. 10C).

Clade 7 (Eutheriini (Camplylochetini + Wagneriini))

Autapomorphies: none. Additional apomorphic character states: scutellum triangular (57: 1); anterior spiracle with slit not closed by fringes of hairs (63: 1); anepimeron with setae presenting various equally strong but not longer than adjacent seta (65:1); posterior spiracle with fringes equally distributed on both sides (67: 1); female terminalia with tergite 7 as 2 broad plates (164: 1); first instar larva with antenna present and well developed (189: 0). In ACCTRAN, wing with bent of M forming a long petiole (longer than r-m) R4+5 reaching wing margin at wing tip (81: 3); male terminalia with membranous connection between basiphallus (dorsal sclerite) and distiphallus immovable (126: 0); distiphallus with acrophallus undeveloped (141: 3).

Eutheriini

Autapomorphies: wing with alula unusually long and darkened (74: 1; fig. 6A); female terminalia with sternite 8 with deeply grooved with lightly sclerotized extension (171: 4); egg with posterodorsal window (181: 2). Additional apomorphic character states: 21 character states.

Clade 8 (Camplylochetini + Wagneriini)

Autapomorphies: pedicel with two strong setae (30: 2). Additional apomorphic character states: head with ocellar setae lateroclinate, in females (5: 1); arista, width in relation to post pedicelum, enlarged, larger (34: 1); wing with discal medial crossvein straight (85: 0); male terminalia with distiphallus with ventral sclerite fused without microtichia to dorsal sclerite (139: 2); first instar larva with posterior spiracle with distal portion of felt chambers darkened (202: 1; fig. 13D);

cephaloskeleton with sclerite of the salivary gland narrow with base enlarged (206: 8). In ACCTRAN, male terminalia with hypandrial apodeme with poorly developed boundary with the central plate (120: 0); distiphallus with extension of the dorsal sclerite with equal length relative to pregonite (134: 0); pregonite lobe-like (150: 3). In DELTRAN, first instar larva with posterior spiracle with slits round with darkened and broad borders (201: 3; fig. 13D).

Campylochetini **tribe rev**.

Autapomorphies: male terminalia with phallopodeme with intermedium pad like with microtrichia (30: 2); distiphallus with acrophallus presenting globose expansion (141: 2); pregonites fused, encircling phallapodem (146: 3). Additional apomorphic character states: 17 character states.

Wagneriini **tribe rev**.

Autapomorphies: none. Additional apomorphic character states: parafacial with setulae (21: 2; fig. 4B); gena greater than the width of the combined length of the scape and pedicel (36: 0); scutellum with various non erected setae in entirely surface (58: 2); abdomen fusiform (90: 4); male terminalia with tergite 6 membranous (99: 2); male terminalia with sternite 6 superimpose at right with segment 7 (111: 1); surstylus, inner side carinate (118: 2); distiphallus bare (143: 1). In ACCTRAN, male terminalia with membranous connection between basiphallus (dorsal sclerite) and distiphallus with 180º movement capacity (126: 1); distiphallus reduced and very elongate, ribbon-like (132: 1; fig. 9E); pregonite elongated, encircling the phalopodem (150: 4). In DELTRAN, pedicel about 3X the length in relation to scape (35: 2); wing with R4+5 vein with setulae beyond the Rs node (78: 1); bent of M forming a long petiole (longer than r-m) R4+5 reaching wing margin at wing tip (81: 3); male terminalia with sternite 6 subsymetrical (109: 2).

Clade 9 (Voriini (Epigrimyiini + Spathidexiini))

Autapomorphies: none. Additional apomorphic character states: dichoptic eyes in males and females (1:0); fronto-orbital plate with orbital setae in males (14: 1); frontal vitta with interfrontal setae (19: 1); male terminalia with ventral sclerite not fused to dorsal sclerite at distiphallus (139: 1). In ACCTRAN, first instar larva with antenna somewhat elongate (190: 2); recurved cephalic organ slightly developed (191: 2).

Clade 10 (Epigrimyiini + Spathidexiini)

Autapomorphies: female terminalia with sternite 8 spatulate (171: 1; fig. 12A) on ACCTRAN and first instar larva with undeveloped posterior spiracle (201: 2), in ACCTRAN and DELTRAN.

Additional apomorphic character states: proboscis with prementum 1x to 0.5 X its length relative to the head (47: 1); female terminalia with sternite 8 with setulae just apically (172: 1). In ACCTRAN, pedicel about 2X the length to scape (35: 0); male terminalia with sternite 6 asymmetrical (109: 0); hypandrial apodeme with poorly developed boundary with the central plate (120: 0).

Epigrimyiini

Autapomorphies: wing with bent of M reaching wing margin at the same point (81:1). Additional apomorphic character states: 17 character states.

Spathidexiini **tribe rev**. (clade 11)

Autapomorphies: none. Additional apomorphic character states: anepimeron with setae slim and short (65: 2); male terminalia basiphallus prolonged to epiphallus (129: 0); distiphallus extension of the dorsal sclerite less than half in length to the median ridge (133: 0); female terminlaia with sternite 9 elongated, same length as the long and modified sternite 8 (176: 2; fig. 12A); first instar larva with antenna present and well developed (189: 0; fig. 14A).

Voriini (clade 12)

Autapomorphies: none. Additional apomorphic character states: 12 character states.

Clade 6 ((Sophiini (Philomyiini + Thelairini)) + (Telothyriini (Eriotrichini (Uramyini + Dexiini))))

Autapomorphies: none. Additional apomorphic character states: male terminalia with basiphallus prolonged to epiphallus (129: 0); distiphallus extension of the dorsal sclerite distally expanded (135: 1); female terminalia with tergite 8 indistinct (165: 1); spermatheca with smooth surface (179: 3).

Clade 13 (Sophiini (Philomyiini + Thelairini))

Autapomorphies: none. Additional apomorphic character states: antenna with plumose arista (33: 2); scutelum with central region presenting setulae (60: 1); scutelum with lateral region presenting setulae (61: 1).

Sophiini (clade 14)

Autapomorphies: none. Additional apomorphic character states: postocellar seta absent (6: 0); frontal setae, ending before the base of antennae insertion (9: 1; fig. 4C); fronto-orbital plate with setulae in males; (12: 0); abdominal sternites 2 to 4 missing (97: 1).

Clade 15 (Phyllomyini+ Thelairini)

Autapomorphies: none. Additional apomorphic character states: anepimeron with setae slim and short (65: 2); male terminalia with pregonite fused completely to middle plate of hypandrium (147: 1); pregonite platiform and weak downward directed (151: 1); first instar larva with recurved cephalic organ slightly developed (191: 2). In ACCTRAN, fronto-orbital plate elevated to the antennal axis (10: 1).

Phyllomyini **tribe rev**.

Autapomorphies: none. Additional apomorphic character states: proboscis with prementum 1x to 0.5 x to the head length (47: 1); female terminalia with sternite 8 spoon-like (171: 6); first instar larva with antenna present and well developed (189: 0). In ACCTRAN, spermatheca with surface presenting high roughness (179: 2), in DELTRAN, fronto-orbital plate elevated at the antennal axis (10: 1).

Thelairini

Autapomorphies: none. Additional apomorphic character states: male terminalia with epandrium lobe-like expansion on inferior lateral margin (113: 0; fig. 8E); distiphallus with extension of the dorsal sclerite less than half to the median ridge (133: 0); distiphallus with the extension of the dorsal sclerite equal sized along its extension (135: 0); distiphallus with ventral sclerite not fused to the dorsal sclerite (139: 1); distiphallus with acrophallus as a granular structure (141: 1; fig. 10A); first instar larva with conic antenna (190: 1; fig. 14A); posterior spiracle with felt chambers at the level of the cuticle (203: 0; fig. 14A). In ACCTRAN, wing with R4+5 vein with setulae beyond the Rs node but before r-m (78: 1).

Clade 16 (Telothyriini (Eriotrichini (Uramyini + Dexiini)))

Autapomorphies: none. Additional apomorphic character states: proboscis with prementum 1x to 0.5 X its length relative to the head (47: 1); abdomen with syntergite 1+2 presenting median excavation until the posterior margin (91: 0); male terminalia with distiphallus with acrophallus reduced as a small somewhat sclerotized structure (141: 0). In ACCTRAN, facial ridge evenly concave (27: 0).

Telothyriini

Autapomorphies: thorax with seta ramificated (48: 2; fig. 5A). Additional apomorphic character states: 13 character states.

Eriotrichini **tribe rev**.

Autapomorphies: none. Additional apomorphic character states: fronto-orbital plate with setae in males (12: 0); facial ridge with the setulae above vibrissae insertion longer, about ½ of vibrissae length (41: 1); scutelum with lateral region just with setulae (60: 1).

Clade 19 (Uramyini + Dexiini)

Autapomorphies: first instar larva with segment V with dorsal microtrichia (194: 2). Additional apomorphic character states: antenna with arista micropubescent (33: 1). In ACCTRAN, facial ridge convex (in lateral view) (27: 1); male terminalia with epandrium presenting a lobe-like expansion on inferior lateral margin (113: 0).

Uramyini (clade 18)

Autapomorphies: none. Additional apomorphic character states: antenna with scape raised (31: 0; fig. 4A); first instar larva with cephaloskeleton presenting the sclerite of the salivary gland subsquared (206: 5); intermediate region with median enlargement (210: 0). In DELTRAN, male terminalia with epandrium presenting a lobe-like expansion on inferior lateral margin (113: 0).

Dexiini (clade 20)

Autapomorphies: none. Additional apomorphic character states: parafacial about the same 1X to 1.5X the width in relation to postpedicelum (20: 1); anepimeron with various equally strong but not longer than adjacent setae (65: 1); male terminalia with distiphallus equal sized along its extension to the dorsal sclerite (135: 0); first instar larva with small and irregular plates dermal cuticle (182: 2); segment XII with sensorial stylus (199: 1; fig. 13B); posterior spiracle with felt chambers in a tubular process (203: 2; fig. 13C). In ACCTRAN, lower facial margin not prominent (29: 1).

Clade 21

Autapomorphies: none. Additional apomorphic character states: frontal setae ending before the base of antennae insertion (9: 1; fig. 4C); parafacial bigger, more than 2X the width in relation to postpedicelum (20: 2; fig. 4E); male terminalia with surstylus broad, massive (116: 0; fig. 8A); phallopodeme with intermedium without specialization (124: 1); distiphallus with acrophallus as a granular structure (141: 1; fig. 10A); pregonite platiform, with strong sclerotifization anteriorly (150: 0; fig. 10D); pregonite platiform and strong downward directed (151: 1); first instar larva with integument presenting sensila (188: 0); segment V with microtrichia located dorsally and ventrally (194: 0). In ACCTRAN, lower facial margin not prominent (29: 1).

Clade 22 – former Doleschaliini

Autapomorphies: ocellar triangle with 2 ocellus (4: 2); fronto-orbital plate about ½ the head length in profile (11: 1); abdominal tergites subparallel-sided (89: 1). Additional apomorphic character states: 11 character states.

Clade 24 – former Rutiliini

Autapomorphies: first instar larva with long spine-like microtrichia ventrally (192: 1). Additional apomorphic character states: wing with vein rm sinuouse (83: 1); male terminalia with granular structure of acrophallus shorter, about half the size the length to extension of the dorsal sclerite (142: 2); first instar larva with small irregular plates (182: 2); polygonal cuticular plates (186: 1; fig. 14C); cuticular plates only on anterior portion (187: 1); cephaloskeleton with mouth hook large, quadrate (207: 3).

Capítulo 3

Brief history of Neotropical Dexiinae, with emphasis on the Latin American tachinodologists

Resumo

O conhecimento da diversidade e história de Dexiinae na região Neotropical, em contraste com outras regiões, por exemplo, a Paleártica, é pouco conhecida. A história deste táxon aumentou gradualmente desde o século 18 a partir dos trabalhos de autores europeus e norte-americanos como J. C. Fabricius, C. R. W. Wiedemann, J. B. Robineau-Desvoidy, P. J. M. Macquart, J. M. F. Bigot, F. Walker, V. von Röeder, E. Giglio-Tos, Brauer and Bergenstamm, F. M. van der Wulp, C.H. Curran, J. M. Aldrich, C.H.T. Townsend, H. J. Heinhard e W. R. Thompson. Somente na primeira metade do século 20 é que surgiram os cientistas nascidos ou estabelecidos na América do Sul. Dipteristas como Jean Brèthes e E. E. Blanchard da Argentina, R. E. Cortés Peña do Chile e J. H. Guimarães do Brasil, são os nomes mais expressivos, não só para os Dexiinae Neotropicais, mas, de fato, para toda a família. Aqui, uma breve revisão cronológica de Dexiinae com base em uma revisão da literatura será discutida. A história foi dividida em quatro períodos. Os períodos correspondem ao período pré-lineano dos séculos XVI e XVII, início do século XVIII, século XIX e primeira metade do século XX. Até a primeira metade do século XX a ênfase estará voltada para os dipteristas europeus e norte-americanos. Posteriormente, com a primeira aparição dos dipteristas sul-americanos, a ênfase será direcionada a eles. Finalmente, algumas notas bibliográficas serão fornecidas para o tcheco Dominik Bilimek, um pouco conhecido coletor do século 19 e Fritz Plaumann, um conhecido imigrante alemão que coletou no Brasil durante o século XX.

Abstract

The knowledge of Dexiinae diversity and history in the Neotropical Region, in contrast to other regions, e.g., Paleartic region, is poorly recorded. The history of this taxa has gradually increased since the 18th century from the works of European and North American authors such as J. C. Fabricius, C. R. W. Wiedemann, J. B. Robineau-Desvoidy, P. J. M. Macquart, J. M. F. Bigot, F. Walker, V. von Röeder, E. Giglio-Tos, Brauer and Bergenstamm, F. M. van der Wulp, C.H. Curran, J. M. Aldrich, C.H.T. Townsend, H. J. Heinhard and W. R. Thompson. Only in the first half of the 20th century that scientits, born or established in South American, became to appear. Dipterists like Jean Brèthes and E. E. Blanchard from Argentina, R. E. Cortés Peña from Chile and J. H. Guimarães from Brazil, are the most expressive names for, not only to Neotropical Dexiinae, but, indeed for the whole family. Herein a brief chronological review of Dexiinae based on a literature review will be given. The story was divided into four periods. The periods correspond to the pre-Linnaean period of the 16th and 17th centuries, the earlier 18th century, the 19th century and the first

half of the 20th. Until the first half of 20th the emphasis will be focused to the European and North American Dipterists. Later, with the first appearance of the South American Dipterists, the emphasis will be directed to them. Finally, a few bibliographical notes will be given for the Czech Dominik Bilimek, a poorly known collector from the 19th century and Fritz Plaumann, a well known German immigrant who collected in Brazil during the 20th century.

> "NEVER does nature seem more beautiful than in the tropics. Anyone with a passion for natural history must try and visit the tropics and experience Earth's most diverse ecosystems firsthand... Alexander von Humboldt, Henry Walter Bates, Charles Darwin, Alfred Russel Wallace, Louis Agassiz, Thomas Belt, Charles Waterton, William Beebe, Frank M. Chapman, and other eminent naturalists have each been profoundly influenced in their beliefs about natural history by visits to the Neotropics."
>
> John C. Kricher, in A Neotropical companion: an introduction to the animals, plants and ecosystems of the New World tropics. Princeton University Press, Princeton, New Jersey. 436p. 1989.

1. Introduction: Neotropical Diptera

The Neotropical region corresponds to the tropical areas that includes South America, Central America and southern and central Mexico, the Antilles (Morrone, 2014) in addition to the Andean region. The taxonomic study of the Neotropical Diptera began, naturally, from contributions by Carolus Linnaeus, especially throughout the various editions of his *Systema Naturae,* and as soon as this work was published, the shortfalls and obstacles appeared for the future Latin American scientists. As an example, beginning with Linnaeus, in the course of the long history of descriptions and collection made by, mostly, Europeans at the Neotropics, the determination of the type localities of material described especially throughout the 18th and 19th were unprecise, being refereed as "America Meridionalis[19]" (South America). Those problems were dealt, for instance, by the publication of Papavero's (1971, 1973) *Essays on the history of Neotropical dipterology*. In his book, the rich and poorly known history of Neotropical dipterology in the 18th and 19th centuries

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[19] Distinction made by Gerardus Mercator in 1538.

were described, including the field trips of early collectors, which can help solving a number of problems on the exact types localities for some species described in the older literature.

Reflecting all the historical and current expeditions to the Neotropics, that resulted in various collections and descriptions, currently there are about 115 families, 2500 genera and 25,000 described species of Diptera from the Neotropical region (Amorim et al., 2002). The first published catalogue of the Diptera for the Neotropical region was published by Papavero during the years of 1966 to 1984 (Papavero, 1966-1984). On the other hand, the catalogue of the North American Diptera was published by Osten-Sacken in 1858, thus, more than 100 years separate the first catalogue of Diptera from North America in relation to South America. Even if the amount of investigation on those regions is highly disproportionate, the Neotropical catalogue, although outdated now, established a groundbreaking advance for the studies of the Neotropical taxa of Diptera with its 102 published fascicles and 2877 printed pages. As argued by Papavero & Amorim (2007), this catalogue provides a significative contribution to the study of the systematics and taxonomy of the Neotropical Diptera. Thus in the 21st century, we could see a significant increase in the number of described species and genera (and even families) being published by native workers, aligned with the development of Diptera collections and the increase in the number of specialists, mainly in Brazil. The importance of the knowledge of its fauna is straightforward in another way: due to habitat destruction, environmental change, and invasive species (Cardinale et al., 2012), species are going extinct so rapidly that many believe we are on the brink of a sixth mass extinction event (Barnosky, et al. 2011). At the estimated current rate of extinction, 70% of species may be gone in just three hundred years (Wheeler, 2020). This loss of biodiversity is a huge problem for tachinid taxonomists, as a great deal of biodiversity, that constitutes their primary data, will remain hidden. For instance, we will be missing a large number of species for most groups, taking with them irreplaceable evidence of their uniqueness and phylogenetic history, besides their potential applicability to human healthy and economy. This trend, that became known as "taxonomic impediment" (mainly due to this biodiversity crisis), is currently occurring with the Neotropical Diptera.

One of those families of Neotropical Diptera that is well known for its diversity in the Neotropics is Tachinidae. This family presents 1053 endemic genera in the world, of which 595 (O'Hara et al., 2020) are from the Neotropical region (corresponding to 76%). Four subfamilies have traditionally been recognized in Tachinidae: Exoristinae, Phasiinae, Tachininae and Dexiinae (O'Hara et al., 2020). The last one, is composed of 1394 species with world wide distribution, of those, 584 species occurs at the Neotropical region, thus corresponding to 41.9% of the total diversity. Hence, the Neotropics are a great source of studies for dexiines.

As a way to overcome the difficulties imposed by the contingency of history (e.g., poorly descriptions with type material deposited in foreign institutions), and the present taxonomic impediment, the theme underlying the present brief historic review is understanding that to know its future one must know the past[20]. Somewhat aligned with this idea, is the thought that the truth of today is the mistake of yesterday, however, a more accurate reflection of history, in a optimistic way, is that the truth of today is the particular case of yesterday. Thus, in order to put these thoughts at work, we can say that the priority that the European scientists had in the 17th and 18th centuries, came from adequate and advanced economic resources, communications, social motivation and technology, all of them absent in the countries of the Neotropical region. Furthermore, the apparent clear mistakes made by those earlier authors must be seen within the time frame of their own epoch. As Pont put it (1996:65): "We all blame the past for what we dislike in the contemporary world - whether it be in Dipterology or in science or in society in general. But there is much that we can admire in the past and much that we can learn from the past, and some basic insights into how the great Dipterists lived and worked, set against contemporary political and social conditions and their own personal circumstances, goes a long way towards explaining why they operated as they did and how features that we perceive as shortcomings entered into their work."

Given this context, the present work provides a bibliographical review on the history of Dexiinae taxonomy at the Neotropical region. This subfamily, as it happens to all Tachinidae, suffers from a taxonomic disharmony in relation to other six biogeographic regions of the world, because of an excessive of genera, and, on the other hand, to a high number of undescribed species. To reach to an approximation of the motives behind these trends is the objective of this essay.

2. Methodology

The present work is the result of a literature review. The story was divided into four periods. The periods correspond to the pre- Linnaean period of the 16th and 17th centuries, the earlier 18th century, the 19th century and the first half of the 20th. Until the first half of 20th the emphasis will

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[20] Phrase attributed to George Santayana, 1863-1952, American philosopher and poet.

be focused to the European and North American Dipterists. Later, with the first appearance of the South American Dipterists, the emphasis will be directed to them.

3. Brief history of Neotropical Dexiinae

Knowledge on Dexiinae diversity in the Neotropical Region has gradually increased since the 18th century. Early taxonomic efforts came from European and North American authors such as J. C. Fabricius, C. R. W. Wiedemann, J. B. Robineau-Desvoidy, P. J. M. Macquart, J. M. F. Bigot, F. Walker, V. von Röeder, E. Giglio-Tos, Brauer and Bergenstamm, F. M. van der Wulp, C.H. Curran, J. M. Aldrich, C.H.T. Townsend, H. J. Heinhard and W. R. Thompson. Only in the first half of the 20th century that authors, born or established in South American, became to appear. Dipterists like Jean Brèthes (1871-1928) and E. E. Blanchard (1895-1971) from Argentina, R. E. Cortés Peña (1915-2001) from Chile and J. H. Guimarães (1937-2008) from Brazil, are the most expressive names for, not only to Neotropical Dexiinae, but, indeed for the whole family. Hence, I will make a brief chronological review of Dexiinae that were described by those European authors of the 18th and 19th centuries in order to, finally, discuss the appearance of the Latin American scientists in the 20th century, that worked with the fauna of Dexiinae of their own region.

3.1. Neotropical Diptera before Linnaeus: the 16th and 17th centuries

The beginning of the Natural history of the Neotropical region starts, naturally, with the most calamitous event in human history (Cornelius De Pauw, in Elliott 1992), the discovery of the New World by Columbus in 1492. A few years after period of conquest and initial settlement, a new epoch considered as ‘natural histories of the New World’, together with an overview of the work on the animals of New Spain (Mexico), inaugurated the interest of the Spanish for the potential benefits that could be derived from the knowledge of the plants and creatures of the Neotropics (Asúa & French, 2005). One of these works is the *General and Natural History of the Indies* that consists of 50 books written by Francisco Fernández de Oviedo (1478-1557); he is one of the most famous of the early chroniclers of the Indies (Asúa & French, 2005). The first part of his book, dealing mostly with the island of Hispaniola (that included zoological data), was published in Seville in 1535. As most of the people from his time, Oviedo employs the fauna of Spain as a term of comparison for describing the appearance and qualities of New World animals. He is the responsible for one of the first relate of flies of the New World, in Hispaniola (current Haiti and Dominican Republic); in it (Book XV, Chapter 3) he made very brief observations about the resemblance with the flies of the

Spain, and noted its behavior and that they can be found in great numbers: "…so many types and varieties that one could go on writing about them forever." Later, most of the references to Diptera were related to attacks of bloodthirsty dipterans (e.g., Culicidae, Ceratopogonidae), as told, mainly, by the second half of the 16th century jesuit missionaries sent to Brazil (Papavero & Couri, 2012a). For instance, the first oldest citation of Diptera in Brazil was made for mosquitoes (in 1552) by Father Francisco Pires (Papavero & Couri, 2012a).

Only at the 17th century that a new view of insects began to develop. Not only the importance of medical and economic aspects of insects were dealt; the scientists began to study others species as well; for curiosity, of by the need to know better the natural history of their New World colonies. According to Papavero & Couri (2012b), the works of Piso and Marcgrave, as scientists working for Johan Maurits van Nassau in Brazil, represent the third oldest publications including illustrations of insects and many of their descriptions and information were not exclusively based on the beneficial or malefaction aspects of insects to man. One of the antecedent works are the drawings of a bee by Stelluti in 1625, in a short treatise on bees entitled *Apiarium*, written by Cesi. However, Stelluti in 1630 (Bardell, 1983) made a drawing of a weevil, hence, being the second oldest illustration. The next work that presents an illustration of an insect, this time a Diptera, is the *L'occhio della mosca* (The Eye of the Fly) by Gioanbatista Battista Hodierna (1597-1660), published in 1644 (Bardell, 1993). The author described and drown the microscopic structure of the eye of the fly. Thereby, the work contained at the *Historia naturalis Brasiliae* is the fourth oldest publications including illustrations of insects, and the first from the Neotropical region. These drawings (fig. 1A, B), that were done with the help of a microscope (Papavero & Couri, 2012b), consists, among other insects, of the first description and illustration of Diptera: a Dolichopodidae (Marcgave, 1648: 253) and a Culicidae (Marcgrave, 1648: 257). It would take almost 200 year to the first dexiine became drawn; this effort was made by Macquart in 1846 (more on this scientist will be given herein).

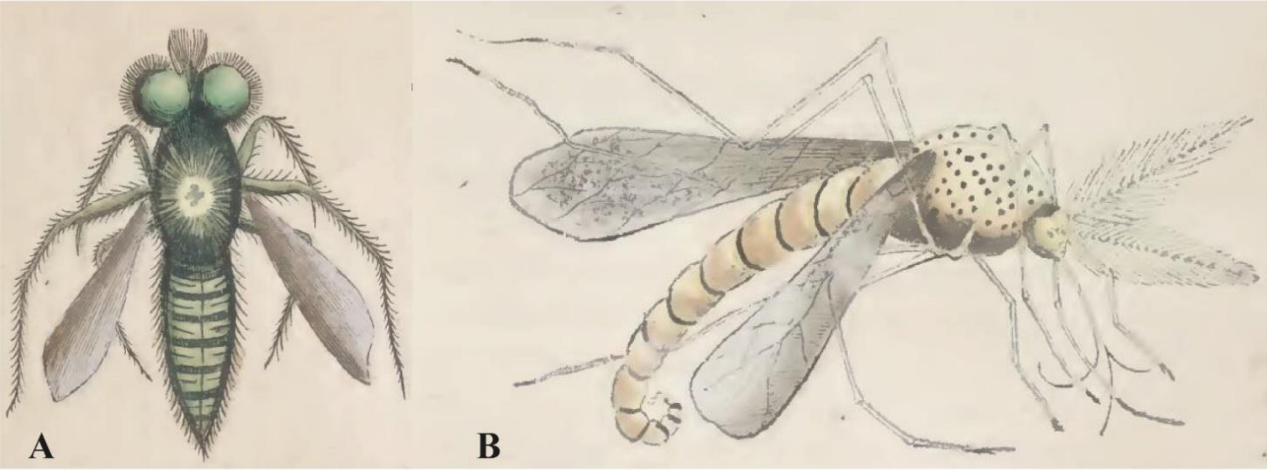

Figure 1. A, Dolichopodidae; B, Culicidae, from *Historia Naturalis Brasiliae* (1648).

3.2. Earlier days of Linnaeus and post-Linnaean era: the 18th and 19th century and the first Neotropical Dexiinae

Binominal nomenclature for scientific names of animals is deemed to have started on January 1, 1758, with the 10th edition of Linnaeus's *Systema Naturae*. As a natural consequence, this publication was the official start of the modern understanding of flies and their classification. Hence, he divided nature into three kingdoms, many classes, orders, genera, and species; flies were placed in the order Diptera in the class Insecta. Linnaeus divided the order into 10 genera and 191 species, and from those species, only 8 were from the Neotropical region (Suriname and Venezuela). Those species were collected from two of his disciples: the Swedish naturalists Pehr Löfling (1729-1756) and Daniel Rolander (c.1722–1795).

Löfling was the first naturalist, with scientific formation, to collect Diptera at South America (Papavero, 1971), more precisely, in Venezuela (for almost two years). He was one of the Linnaeus' students and as a result of this expedition, that ended abruptly with his death in 1756, he collaborated with the 10th edition of *Systema Naturae* with one species of Diptera: the Tabanidae *Tabanus occidentalis* Linnaeus, 1758. View as Entomologist by Linnaeus (Evenhuis et al., 2010), Rolander is referred in eighty-five insects, of which, 4 are Diptera that were described due to Rolander collecting. These species were a result of his seven-month expedition on Suriname and 10 days in St. Eustatius. The following species were described by Linnaeus: *Tabanus antarcticus* Linnaeus, 1758, *Tabanus exaestuans* (current in *Leucotabanus exaestuans* L.), *Tabanus fervens* Linnaeus, 1758 (current in *Phaeotabanus fervens* L.), *Tabanus mexicanus* Linnaeus, 1758 (current in *Chlorotabanus mexicanus* L.) in Tabanidae; *Musca leprae* Linnaeus, 1758 (current in *Hippelates leprae* L.) *Nomen dubium* in Chloropidae. The last two species are doubtfully collected by Rolander: *Musca aequinoctialis* Linnaeus, 1758 *Nomen dubium* in Stratiomyidae, collected by Dahlberg or

Rolander according to Papavero (1971) and *Musca illucens* Linnaeus, 1758 (current in *Hermetia illucens* L.) in Stratiomyidae, collected by Dahlberg or Rolander according to Papavero (1971).

One of most known students of Linnaeus is Johann Christian Fabricius (1745-1808). He took the responsibility to continue Linnaeus work with the insects. He dealt with Diptera in his *Systema Antliatorum* (Fabricius, 1805), in which it contained 1,151 species of flies, distributed among 78 genera (Evenhuis et al., 2010); among those species, the first dexiines derived from the Neotropical region were described. A peculiarity, is that this early work was made before the description of the type genus of Dexiinae, *Dexia* Meigen, 1826, and the definition of group Dexiariae of Macquart (1844), the Dexiinae of today. Hence, almost all Dexiinae were described in other genera, with the majority of them in *Musca* Linnaeus, 1758: *Rhamphinina pica* (Fabricius, 1805), *Scotiptera venatoria* (Fabricius, 1805), *Trichodura anceps* (Fabricius, 1805), *Comatacta variegata* (Fabricius, 1805), *Comatacta tricincta* (Fabricius, 1805) and *Zelia lateralis* (Fabricius, 1805) were all originally described in *Musca*. Just one Neotropical Dexiinae was described in another genus: *Dictya uncana* Fabricius, 1805, current *Oestrophasia uncana* (Fabricius, 1805).

The blatant fact, is that all of these species were described from the vaguely location of "America meridionali", South America, and collected by Smidt (an almost entirely unknown collector). According to Papavero (1971), those Neotropical species could be from the West Indies islands or some mainland country like Guiana. Thus, the lack of precision of these type localities is notorious.

3.3. The 19th as two trends: the inflation of *Dexia* and the beginnings of the recognition of the unique of Neotropical genera

The first species described in *Dexia* that presents distribution to the Neotropical region, was only described in 1829 by Thomas Say (1787-1834)[21]. He described *Dexia vertebrata* Say, 1829 for Indiana (USA), now a species placed in the genus *Zelia* Robineau-Desvoidy, *Zelia vertebrata* (Say), 1829, and distributed from Guatemala to Mexico (O'Hara et al., 2020). The next year marked the publication of two revolutionary works on Tachinidae and Diptera: the *Aussereuropäische zweiflügelige Insekten* by Wiedemann (1830) and the *Essai sur les Myodaires* by Robineau-Desvoidy (1830). Only by a slightly difference of about 3 months, the work of Wiedemann has

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[21] He is considered as the father of American entomology. In addition, he wrote the first book published in America on insects, *American Entomology* (1824-1828).

priority over Robineau-Desvoidy's (Evenhuis & Pont, 2013). Wiedemann (1830) described 24 species of *Dexia*, from which 16 were collected in the Neotropics. Within those 16 species, 7 are valid species in Dexiini or Sophiini within Dexiinae; *Cordyligaster petiolata* (Wiedemann, 1830) from Brazil, in Sophiini; *Zelia plumosa* (Wiedemann, 1830) from Brazil, in Dexiini; *Zelia potens* (Wiedemann, 1830) from Brazil, in Dexiini; *Zelia limbata* (Wiedemann, 1830) from Brazil, in Dexiini; *Yahuarmayoia phaeoptera* (Wiedemann, 1830) from Brazil, in Dexiini; *Euantha aucta* (Wiedemann, 1830) from Brazil, in Sophiini; *Tromodesiana thomae* (Wiedemann, 1830), from West Indies, St. Thomas, *incertae cedis* in Dexiinae (O'Hara et al., 2020). Although the type localities were more precise, with some species being referred to Brazil, there were no information about the collector or the region of Brazil that based his descriptions; an exception is *Dexia melaleuca* Wiedemann, 1830 (= *Musca venatoria* Fabricius, 1805), now in *Scotiptera* Macquart, 1835, that was collected in Rio de Janeiro state, Brazil. Papavero (1971) affirmed that Wiedemann's collection from Brazil included material from Eschscholtz (that were based on material collected in Santa Catarina state), Sieber, Gomes and Feijó (from Amazonas, Ceará, Pernambuco and Bahia states) and Freyreiss and Westin and von Olfers, Sellow, Bescke and Lund (various regions of the country). Indeed, none of his Neotropical species originally described in *Dexia* survived the passage of time: not a single one of them are still placed in their original genus. Actually, only two of his 24 species are still placed in *Dexia*, i.e., *Dexia lugens* Wiedemann, 1830 from South Africa and *Dexia lepida* Wiedemann, 1830 from Indonesia.

The first author that began to realize that the tachinid fauna, mainly from the Neotropics, is unique and tried to accommodate his species in various new genera was Robineau-Desvoidy (1830). Thus, for instance, he erected 16 genera for his group of Macropodea (Dexiinae, in part), of which 6 are still valid within Dexiinae (*Estheria* R.D., *Dinera* R.D., *Zelia* R.D., *Sophia* R.D., *Rutilia* R.D. and *Billaea* R.D.). *Sophia* and *Uramya* Robineau-Desvoidy, 1830 were the first genera created for species exclusively derived from the Neotropics, more precisely, from Brazil. *Sophia* however, is problematic since of the four species originally described it, only *S. filipes* Robineau-Desvoidy, 1830 is valid; the other three were moved to *Scotiptera* Macquart, 1835 [Dexiini]: *Scotiptera gagatea* (Robineau-Desvoidy, 1830) and *Scotiptera pellucida* (Robineau-Desvoidy, 1830), both unrecognized by Guimarães (1971) and the last one is a synonymy of *Scotiptera venatoria* (Fabricius, 1805) – *Sophia punctata* Robineau-Desvoidy, 1830. The type species of *Sophia*, *S. filipes*, is probably lost and is considered it as an unrecognized species of Sophiini (Guimarães, 1982). On the other hand, *Uramya*, then with a single species, *Uramya producta* Robineau-Desvoidy, 1830, was also described from material collected in Brazil, alongside with *Olinda* *brasiliensis* Robineau-Desvoidy, 1830, now placed in *Uramya*, in addition to the others 32 species currently found in this genus (O'Hara et al., 2020). *Uramya brasiliensis* was collected by Saint-Hilaire, that, accordingly to Papavero (1971), took journeys to the following regions of Brazil in 1816 to 1822: Rio de Janeiro, Espirito Santo, Goiás, Minas Gerais, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul states. The last valid Dexiinae species derived from the Neotropical region described by Robineau-Desvoidy (1830) was *Zelia strenua* Robineau-Desvoidy, 1830 from Haiti, Port-au-Prince, now placed in *Ptilodexia* Brauer & Bergenstamm, 1889 (O'Hara et al., 2020).

Species continued to be named by a few other European scientists, like Pierre-Justin-Marie Macquart (1778-1855), Ermanno Giglio-Tos (1865-1926) and the collaborative works of Friedrich Moritz Brauer (1832-1904) and Julius Edler von Bergenstamm (1837-1896) in the latter half of the nineteenth century.

Giglio-Tos was an Italian entomologist that studied at the University of Turin and was hired at the then Museo Zoologico di Torino, current Museo Regionale Scienze Naturale in Turin, Italy (MRSN), in which he worked with the Diptera collection left by many collectors, like Eugenio Truqui, Henri de Saussure, Adrien Sumischrast and Luigi Bellardi (Papavero, 1973). All of them made extensively collecting in Mexico and gathered a considerable material of Mexican Diptera that are deposited at the MRSN that were worked by Giglio-Tos. Bellardi began to work with this material by the publication of his "Essay of Mexican Dipterology" (1859-1862), but sometime later, he left the study of Diptera to dedicate to work with fossil molluscs and died before he could resume his studies on the Mexican Diptera (Giglio-Tos, 1892). Hence, Giglio-Tos took the responsibility to finish the work began by Bellardi. Giglio-Tos published, in short[22] and concise papers (his "Diagnosis of new genera and new species of Diptera" that began in 1890 and ended in 1893), the descriptions of his new species, to, later, give a more detailed, and useful, descriptions in his "Diptera of Mexico", published from 1892 to 1895. In total, Giglio-Tos described one new genus - *Myioscotiptera* Giglio-Tos, 1893 - and 14 new species with only two synonymies. From those 12 valid species, 6 are still placed at their original genus. He never gave any keys or diagnosis for his new species, thus, the recognition of his taxa can be problematic, for instance, the recognition of *Myioscotiptera cincta* Giglio-Tos, 1893, *Scotiptera cyanea* Giglio-Tos, 1893 and *Hystrichodexia mellea* Giglio-Tos, 1893 are difficulty to identify by relying only on his descriptions. However, he based his descriptions and papers on materials exclusively from a Neotropical region (Mexico), and thus, he is the first author to work exclusively with materials from the Neotropics.

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[22] Giglio-Tos just gave a very brief description in Latin, without any information about the localities.

Our next name in this essay, considered as one of France's greatest dipterists (Evenhuis et al., 2016), is Macquart[23]. When he was hired by the Muséum d'Histoire Naturelle in Paris he began to study the exotic, i.e., non-european, species of Diptera collected by a number of collectors, including the following from the Neotropics: Gay and Fontaine in Chile and Peru, Sylveira, Gaudichaud, Vauthier in Brazil, Leprieur, Leschenault, Doumerc and M.me Rivoire in Guyana; Lebas in Colombia; Richard, Lacordaire and Banon in Cayenne; Plée in the Antilles; De La Sagra, Poey in Cuba; Hogard in Santo Domingo and Beaupertuis in Guadeloupe (Macquart, 1838). As a result of these studies, he published his "Diptères exotiques nouveaux ou peu connus" from 1838 to 1855, in two tomes and five supplements, including 2,390 new species and 219 new genera from almost every family of Diptera known at the time (Evenhuis et al., 2016). His "Diptères exotiques" is considered, in its time, one of the most prodigious taxonomic works on Diptera ever published (Evenhuis et al., 2016). From this great work, we can find almost all Neotropical Dexiinae (just one taxon, *Scotiptera* Macquart, 1835, was described in his "Histoire naturelle des insects"). In total, he described eight genera, of which two is synonymized (*Aporia* Macquart, 1846 = *Uramya* Robineau-Desvoidy, 1830 and *Cordyligaster* Macquart, 1844 = *Megistogaster* Macquart, 1851). In relation to his new species, he proposed 12, of which 2 are unrecognized in Dexiinae; in addition, no synonymies were proposed throughout these years. Finally, as argued by Crosskey (1971), Macquart provided keys and diagnoses for all of his tribes and genera, and his work can be considered very advanced and of great quality for his time. Finally, as a historical element, Macquart (1846) was responsible for the first drawing of a Neotropical Dexiinae: *Uramya quadrimaculata* (Macquart, 1846) (2B), *Ebenia claripennis* Macquart, 1846 (2A) and *Ptilodexia rubriventris* (Macquart, 1846).

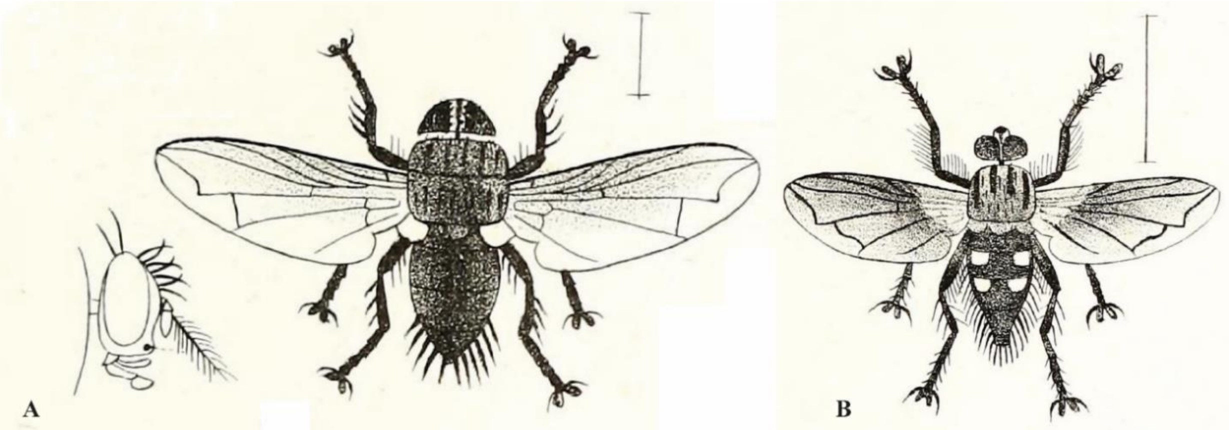

Figure 2. A, *Ebenia claripennis* Macquart, 1846; B, *Uramya quadrimaculata* (Macquart, 1846).

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[23] An extensive literature from his life and work can be found in his autobiography (Macquart, 1849) and in the work of Evenhuis et al. (2016).

In the only cooperative work discussed herein, the contributions of the Austrians Friedrich Brauer and Julius von Bergenstamm will be briefly exposed. This brief history of this partnership began in 1861, when Brauer accepted a position at the Kaiserlichen Museums zu Wien, now Naturhistorisches Museum, in Vienna and he was named curator of the entomological section in 1876. Beginning in 1880, he started publishing his monumental work on the Diptera of the Museum of Vienna ("*Die Zweiflügler des Kaiserlichen Museums zu Wien*"). Later, continuing with this work, he began a series co-authored with Julius von Bergenstamm on the higher Diptera excluding the Anthomyiidae [his "*Muscaria Schizometopa (exclusive Anthomyidae*)"]. Four parts of this series on higher Diptera were published, constituting the parts parts IV-VII, from 1889 to 1894. In this work, they could see a great number of types from Schiner, Egger, Wiedemann, Meigen, present at the Museum of Vienna, and Robineau-Desvoidy, Macquart and Rondani types that were from the particular collection of Julius von Bergenstamm and Bigot. Thus, this partnership was much a matter of necessity, as Julius von Bergenstamm had these valuable types that Brauer considered invaluable to finish his work (Handlirsch, 1905). Consequently, Handlirch (1905) regard this work, both in merit and intellectually, to Brauer only.

Brauer and Bergenstamm (1889-1895) described over 250 genera and subgenera of Tachinidae, of which 99 are currently valid genera (O'Hara, 2013). In relation to Neotropical Dexiinae, a peculiar trend can be found: they described 20 new genera, and 16 new species. From those 20 genera, three are invalid and from those 16 species, five are invalid, a high number, consisting of about ¼ of their new species. This is surprising, because they had access to the aforementioned types, and yet have made constant mistakes when describing new species. A number of them were synonymous with species that they, very probably, have seen; for instance, synonymies with Wiedemann's and Bigot's species are a particular trend found in Brauer and Bergenstamm's work. Finally, in relation to the type localities found on their work, a recurrent collector, in a recurrent country, are found for various taxa. The name of Bilimek and the country of Mexico is constant in their work[24], so much that two species were named after him: *Prorhynchops bilimeki* Brauer & Bergenstamm, 1891 and *Ormia bilimekii* (Brauer & Bergenstamm, 1889). As there are some scattered and very brief records of his life and travels (see, for instance, Papavero, 1973: 291-292), a few notes and records of his life as a naturalist will be given.

Dominik Bilimek, born Adolph Joseph Bilimek, was born in 1813 in Nový Jičín a town in the Moravian-Silesian region that is currently in Czech Republic. In 1832 he entered the Cistercian

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[24] In relation to the Neotropical dexiines, four species were collected by Bilimek from Mexico (in Mazatlan or Takubaya).

monastery of Wiener Neustadt being ordained a priest in 1837, where he took the name of his father Dominik (Polách, 2013). Even as a young priest, Bilimek always found time for the natural sciences; soon, entomology and speleology became his new passion. His interest in science grew to a highly professional level, for instance, in 1851 he attended the inaugural meeting of the Zoological and Botanical Society in Vienna (Polách, 2013) and, in the same epoch, he came into contact with naturalists, including the important Viennese geologist Eduard Suess (Roth, 2019). Later he was a teacher at the Military Academy from 1854 to 1864 in Cracow, Hainburg, Strasbourg, Eisenstadt and Wiener Neustadt. During this period, he worked on archaeological research and excavations and made the acquaintance with Austrian archduke Ferdinand Maximilian Joseph (1832-1867), a contact that would chance his life. Ferdinand Maximilian invited him, in 1865, to go to Mexico where he was declared as Emperor of the Second Mexican Empire (1864-1867), to found the natural history collection of the Imperial Mexican Museum. Bilimek accepted the invitation (and adventure) and was appointed curator of the Department of Natural History of the National Museum, where he was in charge of supervising the organization of archaeological and ethnographic objects and books, in addition to the fauna and flora specimens (Polách, 2013).

In the spring of May of 1865, Dominik Bilimek arrived in the Mexican port of Veracruz, from where he traveled to Mexico City (Polách, 2013). Immediately upon his arrival, he took on duties on the museum and began his first research surveys around the royal Chapultepec Castle (residence of archduke Ferdinand Maximilian and his Empress Charlotte). On his collecting trips around the city and near the Chapultepec Castle, Bilimek was often accompanied by the Empress Charlotte and her ladies-in-waiting (Polách, 2013), collecting together natural history material for the museum. On January of 1866, together with Emperor Maximilian, Bilimek visited the famous Cacahuamilpa caves (in Guerrero State, south of Cuernavaca), one of the largest cave complexes in the world, which is still sought by speleologists from around the world (Gómez-Aguado et al., 2016). From their speleological surveys, the first biological investigation of a cave in Mexico (Palacio-Vargas et al., 2015), Bilimek (1867) prepared an article called "Fauna der Grotte Cacaliuamilpa in Mexiko" [Fauna of the Cacaliuamilpa cave in Mexico], in which he described, although he was told that nothing living could be found inside the cave, the happyness to found living animals within it. Although not able to explore the entire cave (he stayed on the 14 of January from 8 a.m. to 3 p.m.), he could find "under the stones and on the stalagmites" 11 animals, of which 10 were described as new by him, including: Coleoptera (Carabidae and Catopidae), Lepidoptera

(Gracillariidae), Diptera[25] (Milichiidae), Orthoptera (Rhaphidophoridae), Blattaria (Polyphagidae), Thysanura (Nicoletiidae), Amblypygi (Phrynidae), Araneae (Gnaphosidae and Pholcidae) and Isopoda (Armadillidae). For this scientific publication, Bilimek received the Emperor's Gold Medal for Civil Merit (Polách, 2013).

However, everything changed within a few months after this article. A civil war broke in Mexico, with the Mexican republican forces, with the aid of the United States, expulsing the French troops in 1866, so that finally, the Empire came to an end on June 19, 1867 when Emperor Maximilian was executed and the government restored the Mexican republic. In the middle of this, Dominik Bilimek had to organize, very quickly, his departure from dangerous Mexico, including the transport of his collections, notebooks and notes. As a precaution, Emperor Maximilian appointed Bilimek as director of the Natural History Museum of the Miramare Castle in Austria (that was built by Maximilian and his wife), by decree, so that he obtained civil servant status (Roth, 2019). The emperor's death caught up with him while hiding in Orizaba (Polách, 2013), but, thanks to an English ship, part of the collections traveled to Europe from Veracruz. Thus, when Bilimek returned to Europe he fulfilled the wish of Maximilian and became the director of the museum at the imperial residence in Miramar near Trieste (Italy). As the custodian of the museum, Bilimek undertook scientific trips to Sweden, Norway, Italy, Palestine, Egypt and Algeria (Polách, 2013).

The collections of Dominik Bilimek are scattered throughout many museums and countries around the world. Bilimek's botanical collections are kept at the Natural History Museum (UK) and Kew Royal Botanic Gardens in London, Muséum d'Histoire Naturelle in Paris and Lyon; there are also specimens in the United States, such as the herbarium of the Smthisonian Museum in Washington and at Harvard University, Cambridge; in addition to the ones in St. Petersburg (Polách, 2013). In relation to his invertebrate collections, mainly insects, are deposited in Vienna (NMW). Due to his age, he finally retired to Vienna and lived on the monastery of his Cistercian order in Neukloster, where he died on August 3, 1884 from a stroke. His grave is in the forest cemetery near Heiligenkreuz (Roth, 2019).

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[25] This species is *Pholeomyia leucozona* Bilimek, 1867. Bilimeki found this taxon "Swarming around on stalagmites in the Cacahuamilpa cave in Mexico."

Figure 3. Photograph of Dominik Bilimek. Availed at: http://www.zisterzienserlexikon.de/wiki/Bilimek,_Dominik

Back to the Dipterists. Within this same epoch, the British dipterist Francis Walker (1809-1874), in opposition to the approach of Robineau-Desvoidy, tried to include a wide range of different species within his large definition of *Dexia*. As a straightforward example, from 74 species of *Dexia* described by Walker throughout his career, only 38 are still valid species placed in various genera and tribes in Dexiinae (some species were incorrectly considered as Tachinidae, and are now placed in Calliphoridae, Mesembrinellidae and Sarcophagidae). From those 38, only 8 are still placed in *Dexia*. Considering the Neotropical taxa, from those species described in *Dexia*, 18 species were from that region, of which 6 are still valid and placed in various places in Dexiinae. Walker's descriptions and species hypothesis are known for being very problematic (Crosskey, 1974), for he described almost all of his species based on only one specimen; thus, every specimen was a species for him (Austen, 1907). In relation to the other species of dexiine described by Walker on other genera, only 6 are valid and placed in this subfamily.

Other dipterist from France that had importance for the Neotropical Tachinidae and Dexiinae was Jacques-Marie-Frangile Bigot (1818-1893). Very little is known about him, however, what is known is that Bigot had a lifelong interest was in the Diptera. Thus, at the age of 26, he became a member of the Societe entomologique de France (Crosskey, 1971), and in the following year (1845) he published the first of his long series of papers on Diptera in the Annales (and associated Bulletin des Seances) of that Society (Anonymous, 1893). The large series "*Diptères nouveaux ou peu connus*" that began in 1874 and had 37 "parts", concluded in 1892, was one of his main works. The species described by him were derived from all parts of the world; however, he is notable for describing various Neotropical genera (mainly for Mexico), exceeding in number from those from other parts of the world. As Crosskey (1971) argued, Bigot toyed with descriptive work at a very superficial level, going as far as to the almost impossibility to recognize any genera or species descriptions made by him without access to his type material[26]. Bigot described various Neotropical taxa of Dexiinae, but only 6 genera and 20 species are still valid. Even with these criticisms, a great advance was provided by Bigot: none of his species were placed in the genus *Dexia,* as it was a common practice by his predecessors. Only when one is able to set aside his superficial and poor descriptions, usually based on single specimens, and seeing his types, that we can see the great work that he has done for the Neotropical Dexiinae. The type localities were a problem however, as in the majority of his species we can only read the country that these specimens were collected.

The last great contribution for the Neotropical Dexiinae from the 19th century came from a work named "Biologia Centrali-Americana" and subtitled as "Contributions to the knowledge of the fauna and flora of Mexico and Central America". This work covered various aspects and groups of animal and plants, including a section on archeology. The importance of this work is so great that Selander & Vaurie (1962:3) consider that: "The 'Biologia Centrali-Americana,' [is] unquestionably one of the most monumental and important faunal works ever published…" This work was organized, directed and edited by two eminent British naturalists Frederick DuCane Godman and Osbert Salvin (Selander & Vaurie, 1962). It was issued on a subscription basis in 257 parts, the first of which appeared in September, 1879, and the last in June, 1915, thus during 36 years in which more material was constantly being added to the collection (Godman, 1915). One remarkable result of "Biologia-Centrali Americana" is the precision of the type localities given by all the species, as these materials were carefully labeled with the name of the settlement or physiographic feature at or near which collections were made (Selander & Vaurie, 1962).

By 1906 there were 17.525 species of Diptera deposited at the Natural History Museum, UK (Godman, 1915), then British Museum of Natural History. All those species of Diptera were treated in "Biologia Centrali-Americana" in 3 volumes and one supplement (to Vol. I). What will interest us here is the portion dealt by the Dutch Dipterist Frederik Maurits van der Wulp (1818-1899), that

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[26] All Neotropical Tachinidae described by Bigot are now deposited at the NHM-UK (Crosskey, 1971), and I could see all the holotypes from Dexiinae and could confirm the views of Crosskey (1971).

wrote the volume II (1888-1900) which dealt with the calyptrates[27]. Van der Wulp was a civil officer in the Dutch Audit Office, from which he retired after 50 years' service, when he was nominated Knight of the Order of Orange-Nassau. On 1845, Wulp was one of the founders of the Nederlandse Entomologische Verening (Dutch Entomological Society). In this time, he began his studies with Diptera, as the majority of the entomologists in the Netherlands devoted their attention to Coleoptera and Lepidoptera. From 1870 to 1894 he was secretary of the same Society and from 1867 to 1894 the editor of its journal, the "Tijdscrift voor Entomologie" [Journal of Entomology], founded in 1858. In 1894 he was elected Honorary Member of the Society (Snellen, 1900). According to Papavero (1973), the greatest part of the syntypes described by Wulp are deposited at the Natural History Museum, London. Wulp described in total 65 species and 12 genera in Dexiinae, from which 62 are still valid and only one of his genera has been synonymized (*Melaleuca* van der Wulp, 1891 = *Zelia* Robineau-Desvoidy, 1830). From those species, only 18 are still placed in their original genus, thus showing some problems with his generic delimitation. As showed, never before we had so much detailed information for type localities for Dexiinae, hence "Biologia" went much further than merely citing the countries of which the species belong; Wulp gave plenty and useful information on various species of Dexiinae for Mexican and Costa Rican[28] specimens. All those species from Mexico were collected H. H. Smith, as it is quoted by Wulp throughout his contribution to the "Biologia" (for more details and a biographic overview of Smith, see Papavero, 1973), while those from Costa Rica were collected by H. Rogers.

3.4. 20th century and the age of multiplicity of new genera

The first half of the 20th century marked the declined of the dominance of Europeans Dipterists, and the increase of North Americans and Canadians that studied the Neotropical Dexiinae. The most important names being Charles Howard Curran (1894-1972), John Merton Aldrich (1866-1934), Charles Henry Tyler Townsend (1863-1944), Henry Jonathan Reinhard (1892-1976) and William Robin Thompson (1887-1972). Curran was Canadian but worked from 1928 to 1960 at the American Museum of Natural History (USA). Throughout his career, he described 650 species in Tachinidae, of which 19 are Neotropical Dexiinae. His major contribution to the knowledge of Neotropical Tachinidae came from his monograph, the Diptera of Kartabo, Bartica District, British Guiana (1934). In this work, he provided keys tachinids from this region, in

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[27] This volume was left incomplete after his death in 1899.

[28] Just two species of Dexiinae were collected from Costa Rica: *Hystrichodexia echinata* van der Wulp, 1891 and *Bathydexia albolineata* van der Wulp, 1891.

addition to keys and good descriptions of his new species; thus, the taxa of Tachinidae worked by him were a reliable source to identify a species (without requiring the consulting of type material). In relation to his taxa prosed as new genera, he described 19 for Dexiinae, in which only 6 were not synonymized (O'Hara et al., 2020), evidencing that, as Wulp and Bigot, most of his new genera does not survived the 21st century. In relation to the Netropical Dexiinae, of the 7 new genera described by Curran, only 3 are still valid today, i.e., *Zonalia* Curran, 1934, *Heliaea* Curran, 1934 and *Jamacaria* Curran, 1928.

The next great Dipterist that will interest us here is the North American John Aldrich. Since 1918, until his death in 1934, he was the Custodian of Diptera and Associate Curator of Insects of the Smithsonian National Museum of Natural History, Washington, D.C., USA. During his time working at the Smithsonian, Aldrich's great contributions to the Neotropical Dexiinae were made. A huge contribution to anyone working with the Neotropical taxa of Tachinidae (even though initially planned to the knowledge of flies from the USA, based on the Smithsonian National Museum of Natural History), were his papers on the types of the New World taxa described by Wiedemann and Brauer & Bergenstamm. Published in 5 papers during the years of 1924 to 1929, the objectives of Aldrich were to redescribed poorly known taxa that could not be properly recognized from those old works. Hence, by giving a detailed and excellent redescriptions, sometimes accompanied by synonymies and invaluable taxonomic notes, to this date the only information for those 22 species of Neotropical Dexiinae were the ones dealt by him. Guimarães (1971), in his Neotropical catalogue, recognized the highly relevance of these works by done by Aldrich, thus for each catalogued by species he would refer to those redescriptions made by Aldrich.

Just two months before Aldrich died, his most comprehensive and remarkable contribution for the Neotropical Tachinidae was published; the Tachinidae part from "Diptera of Patagonia and South Chile based mainly on material in the British Museum (Natural History)" (Aldrich, 1934). Cortés & Campos (1970) considers this work as canonical for the tachinids from Chile and Argentina, in which Aldrich described 140 species in 70 genera. Later, the authors empathize that a great value from his work came for the descriptions and keys for the Dexiini from this south area of the Neotropics. Poorly known genera like *Dasyuromyia* Bigot, 1885, *Psecacera* Bigot, 1880 and *Trichodischia* Bigot, 1885 had their species keyed (sometimes with the type species redescribed), in addition to description of new species; thus, contributing greatly for future workers of this fauna, like Raul Cortés (that will be discussed later). By describing 9 genera of Dexiinae (Aldrich, 1934) from Patagonia, and none invalid to this day, is evidence of the incredible work done by him. Finally, from the years of 1924 through 1934 Aldrich described 15 genera, of which only one is synonymized, i.e., *Opsophagus* Aldrich, 1926 = *Cyrtophloeba* Rondani, 1856 (O'Hara et al., 2020). He achieved great results in relation to his new species as well: in total, he described 39 new Neotropical Dexiinae, and none were synonymized; from those, only 6 species are placed differently from their original designation. Besides all these great achievements, the most notorious fact was the preoccupation of Aldrich to revise some species, and not just to add new taxa to an already inflated Tachinidae. Therefore, he was the first author that worked with the Neotropical Dexiinae that made redescriptions and taxonomic works in addition to describing new taxa.

Nevertheless, all these advances were partially lost when the North American dipterist Charles Townsend, the most productive author to publish at the Neotropical region, entered the scene. From his first Neotropical dexiine described in 1892 - *Microchaetina valida* (Townsend, 1892) from Peru – to his last in 1940 – *Trochilochaeta transcendens* Townsend, 1940 from Brazil – he ended up describing 90 species in addition to the description of 62 genera. One of the main problems, if not created, but increased by Townsend, is the description of excessive number of monotypic genera. Various of his genera became synonymized, sometimes with multiple genera considered as a single one; for instance, Townsend proposed 6 genera (*Eutheresia* Townsend, 1912; *Paratheresia* Townsend, 1915; *Theresiopsis* Townsend, 1916; *Amphiboliopsis* Townsend, 1926; *Bathytheresia* Townsend, 1928; *Philotrichostylum* Townsend, 1933) which were synonymized with *Billaea* Robineau-Desvoidy, 1830 and erected 8 genera (*Phasiodexia* Townsend, 1925; *Eoptilodexia* Townsend, 1926; *Eomyocera* Townsend, 1926; *Sumatrodexia* Townsend, 1926; *Calotheresia* Townsend, 1926; *Eomyoceropsis* Townsend, 1926; *Asbellopsis* Townsend, 1928; *Barydexia* Townsend, 1928) lster synonymized with *Dexia*. In addition, there was not, as it happens today, a unique and workable identification key for supraspecific (and infraspecific) levels; the keys proposed by Townsend (1927), for instance, for all Neotropical Tachindae so far known until the year 1927, are unworkable and almost useless.

Adding to the excess of artificial monotypic genera, another problem with Townsend's approach is his descriptions. The union of a brief and unimportant description of characters with his unique and confusing system of nomenclature (Townsend, 1928), created and used by him in his late descriptions, brought some difficulties in interpretation and identification of his taxa. This system of nomenclature and abbreviations was used in his biggest contribution to Tachinidae: his *Manual of Myiology*, a 12-volume series on the "Oestromuscaria" published between 1934-1942. In this work he produced most of the classification system for the Neotropical Region, that to this date is still the only reference for various genera of Neotropical Dexiinae. However, for such a huge (over 3,000 pages) and comprehensive (all known Oestroidea Diptera know in that epoch) it was highly criticized by being considered incomprehensible and confusing (Mesnil, 1980) or unmanageable and artificial (O'Hara, 2013). On the other hand, even though we can consider Townsend's contribution to Tachinidae and Neotropical Dexiinae as a decline in quality in relation to his contemporaneous Dipterists (mainly to Aldrich), there were some clear advances. The knowledge of the Neotropical diversity of Dexiinae increased, as from the 158 genera currently considered as valid and belonging to the Neotropical Dexiinae, 62 were proposed by Townsend (about 39% of all genera). A great part of those species was collected by Townsend himself during a long term stay to Peru in two periods: one from 1909 to 1914 and the other from 1923 to 1929; and to Itaquaquecetuba (Brazil) where he lived in from 1929 to his death in 1944 (Evenhuis et al., 2015). Thus, he described some rarely collected Neotropical taxa, for instance, *Itamintho erro* Townsend, 1931 (allied to *Phyllomyia*) and *Exodexia uruhuasi* Townsend, 1927 (allied to *Prophorostoma*, Townsend 1927), which were not found in various collection in Brazil. Finally, it will be many years until Neotropical tachinologists will be freed from consulting the *Manual of Myiology* for basing their identifications.

Figure 4. Standing: William Beutenmuller, E. P. Felt, Charles T. Greene, R. C. Osburn, H. S. Harbeck, E. Daecke, C. L. Metcalf, C. T. Brues, F. Knab; Seated: Nathan Banks, **J. M. Aldrich**, C. W. Johnson, E. T. Cresson, **C. H. T. Townsend**; Seated (floor): R. C. Shannon, M. D. Leonard, R. R. Parker, F. L. Thomas. Available at: Smithsonian Institution Archives, SIA Acc. 96-080 [SIA2015-002177], Created by Beutenmüller, William, "Group Portrait of Dipterists", SIA2015-002177, Retrieved on 2020-08-28.

The last North American Dipterist that will be briefly discussed herein is Henry Reinhard. He was an entomologist that joined, in 1919, the Department of Entomology at Texas A&M University, worked at this institution until his retirement in 1960 (Burke, 1977). Reinhard began his career working with biological control of insects, but soon became interested in the taxonomy of flies throughout his professional career (Burke, 1977). He published 107 scientific papers spanning a period of 55 years, describing within these years 94 new genera and 529 new species of Tachinidae and Sarcophagidae (Burke, 1977), of which 10 genera and 40 species are from Neotropical Dexiinae (mainly from Mexico). From his taxonomic revision of *Chaetophlepsis* Townsend, 1915 (= *Campylocheta* Rondani, 1859), *Prosenoides* Brauer & Bergenstamm, 1891 and *Mochlosoma* Brauer & Bergenstamm, 1889, the first ever revisions including Neotropical species of Dexiinae, the knowledge of this taxa was significantly enhanced. His workable keys, in addition to his accurate and detailed descriptions, that have always accompanied his works, contributed greatly to the future generations of tachinidologists, mainly in relation to provide a easily recognition of his taxa. From those 10 new genera of Neotropical Dexiinae, all from Mexico, 9 are still valid, with just one synonymy: *Parcipromus* Reinhard, 1958 = (*Neosolieria* Townsend, 1927).

Before we introduce the Latin American dipterists, let us first discuss the contributions of the Canadian William Thompson. Although first introduced to tachinids by Townsend (Thorpe, 1973), Thompson developed a very different approach to study them. Instead of describing more and more species and genera, he focused on making redescriptions, keys and discussions about the biological knowledge of the first instar larva of tachinids. We could see this approach in his last contribution to the tachinids while working on the Imperial College of Tropical Agriculture in Canada: the "Tachinids of Trinidad" (Thompson, 1961-1968). Published in various journals in North and South American, during 7 years and totalizing 827 pages, marked the end of his work as a scientist (Thorpe, 1973). Two works dealt with dexiines: his first on "the Voriines" and his other on "Echinomyiines, Dexiines, and allies". In addition to giving one of the more workable and clearer keys for Netropical taxa of Dexiinae, one of the most complete and detailed redescriptions (and descriptions) was delivered by him. Another highlight from these works is the section "Taxonomic Relationships" given for the genera that constituted Townsend's tribes; by discussing these groups with the Neartic and Paleartic fauna, he discussed the affinities of those taxa and pointed to new arrangements, for instance, by studying the larvae of some Iceliini, he suggested that their placement as Dexiinae by Townsend does not agreed with the larval characters, and then suggested that they could be better placed in Tachinindae[29]. All those 25 species distributed in 19 genera discussed by him become a reference for anyone working with the Neotropical fauna. Hence, in the same way that happened to Aldrich, all those species worked by Thompson in the “Tachinids of Trinidad” was referred by Guimarães (1971) for each one catalogued by him. Just three years lies between the last contribution of Thompson and the publication of the Neotropical catalogue of Tachinidae by Guimarães (1971), a groundbreaking contribution for the tachinids and dexiines. In the next section, we will discuss this contribution and others made by Latin American scientists.

3.5. Latin American Dipterists enter the scene: Brèthes, Blanchard, Cortés and Guimarães

The first name to contribute to the knowledge of the dexiines from the Neotropics is Jean Brèthes (1871-1928). He was born in Saint Severs, France and at the age of 19, he traveled to Argentina, where he spent the rest of his life. Self-educated in entomology, he was designated in 1902 as the curator of the entomological section in Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN) and later became a professor of Applied Zoology in the University of La Plata (Dallas, 1928). He studied all insect orders, but he specialized in Hymenoptera and Diptera, described in excess of 1,100 species and published more than 200 works (Dallas, 1928). Among his new species, he described four species of Dexiinae (of which are all valid), and just one, *Hystrichodexia pueyrredoni* Brèthes, 1918, have persisted in its original genus[30]. For the first time, types of Neotropical Dexiinae (those described by Brèthes) were deposited at the institutions at the Neotropics, mainly in the MACN (Mulieri et al., 2013). His descriptions were somewhat brief, and his new species were never compared with allied genera or given some kind of a diagnosis, thus bringing some problems to recognize his new taxa. One of his main contribution to the knowledge of the Diptera fauna from Argentina, Paraguay and Uruguay was his “Catálogo de los dípteros de las Repúblicas del Plata” (Brèthes, 1908). This work was an actualization of the last catalogue published by Enrique Lynch Arribálzaga (1882)[31], that covered the Diptera of parts of Argentina and Uruguay. Brèthes (1908) listed 8 species of Dexiinae – none described by a Latin American author – of those only 2 (*Zelia plumosa* (Wiedemann, 1830) and *Ptilodexia argentina* (Bigot, 1889)) are still valid, with one species (*Melanophora americana*

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[29] This suggestion was later confirmed by Guimarães (1976).

[30] Though the kindness of Dr. Mulieri, I could study some photographs of this species. I could conclude that is not an *Hystricodexia*, but very probably, it could be a *Ptilodexia*.

[31] According to Amorim (2009), this was the first regional catalogue of Diptera from the South America.

Macquart, 1843 = *Melanophora roralis* (Linnaeus, 1758) in Rinophoridae, and the remaining species being whether unrecognized species of Dexiinae or unplaced Tachinidae (Guimarães, 1971).

Although he was not so important for the dexiines, he contributed largely to the Entomology of Argentina, where he was a founder member of the Entomological Society of Argentina. In addition, he received the title of *Doctor Honoris causa* from the University of San Marcos in Peru (Dallas, 1928). Indeed, he was deeply attached by his origins, as the most of his descriptions were written in French. However, this fact does not diminished his influence in Argentina as Ducloux (1928: 6) wrote about him: "...la fauna argentina le proporcionó los temas de sus investigaciones... no dudo en llamarlo con justo título entomólogo argentino, profesor nuestro, colaborador valioso en la obra de nacionalidad, en la formación de nuestra propia cultura. ["…the Argentine fauna provided the subjects of his research… I do not hesitate to call him with a fair title of Argentine entomologist, our teacher, valuable collaborator in the work of our nationality, in the formation of our own culture.].

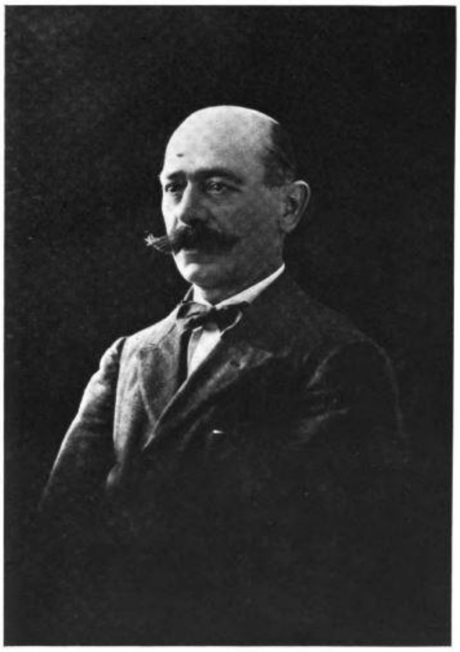

Figure 5. Jean Brèthes. Photograph from Ducloux (1928).

The Argentinean Everard Blanchard (1895-1971) was also a distinguished entomologist in his country. This view is confirmed by Pirán (1972: 29) who considered him: "… indiscutiblemente una de las figuras señeras de la entomología argentina. [… indisputably one of the leading figures of Argentine entomology.] Although born in Argentina (Buenos Aires), he concluded his studies in the United States, at the University of Maine, where he graduated as an entomologist (Pirán, 1972). Blanchard worked for more than 30 years at the "División de Zoología Agrícola, Ministerio de Agricultura y Ganadería" and later was the director of the "Instituto de Patología Vegetal" (Pirán, 1972).

As Brèthes, he studied various insect orders, but specialized, mainly, in Diptera. He described numerous species of flies, mostly on Tachinidae and Sarcophagidae, and published more than 150 articles (Cortés, 1973a). One of the main contributions made by him was the description of the first genus of Neotropical Dexiinae: *Parabillaea* Blanchard, 1937, however, it is synonymized with *Billaea* (Guimarães, 1971). The second (and third) older valid genera of dexiinae are *Actinoplagia* Blanchard, 1940 and *Prosenactia* Blanchard, 1940. These are poorly known genera that had never been comparatively studied, and as a result, some authors changed their placement: *Actinoplagia* was first described as belonging to Actiini (Siphonini in part), then Guimarães (1971) transfer it to Germariini, finally O'Hara (et. al., 2020) placed it in Voriini; *Prosenactia* was also first described as belonging to Actiini (Siphonini in part), then Guimarães (1971) transfer it to Siphonini, to finally O'Hara (et. al., 2020), once again, placed it in Voriini[32]. *Neopaedarium* Blanchard, 1943, on other hand, is a less problematic genus being placed in Voriini since its initial description. In total, Blanchard described six genera in Dexiinae, with five valid to this date (O'Hara et al., 2020), in addition to his nine new species, just one is doubtfully placed in synonymy[33]. Blanchard's descriptions are one of the clearer and more detailed found for dexiines, comparable with the ones given by Thompson. Another clear advancement, mainly in relation to Brèthes, was that he gave tribal placements and discussed the close genera in his descriptions (that would base his diagnosis). An unprecedented novelty was that most of his new species presented host records, perhaps due to Blanchard's interests in Agriculture and for working in an institution that researched in this area. However, a clear disadvantage was his close relation and use of Townsend's works. The confusing nomenclature and abbreviations used by Townsend were also used by Blanchard in his descriptions. In addition, he was a "splitter" in the same (or even worst) "philosophy" of

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[32] I was able to examine a small series of *Actinoplagia koehleri* Blanchard, 1940 at NHM-UK. This species resembles very much with the genus *Germaria* Robineau-Desvoidy, 1830. As *Prosenactia liebermanni* Blanchard, 1940 is very close to *Actinoplagia* (as stated by Blanchard), both genera appear to not belong to Voriini, but somewhere near Germariini (Tachininae).

[33] *Voria ayersai* Blanchard, 1943 was put as a doubtful synonymy with *Voria ruralis* (Fallen, 1810) by Guimarães (1971). Fleming et al (2017) put this species as a definitive synonymy with *Voria ruralis*. However, they did not see any type, or discussed the reasons for this act. Thus, the status of a doubtful synonymy with *Voria ruralis* is better to be maintained as it seen premature to make this move without further studying this species.

Townsend. Hence, as it happens to Townsend, probably his genera were unnecessarily created and most of it will end up in synonymy. Finally, he had three species described in his honor, including the dexiine *Ateloglutus* (*Ateloglutus*) *blanchardi* Cortés, 1979.

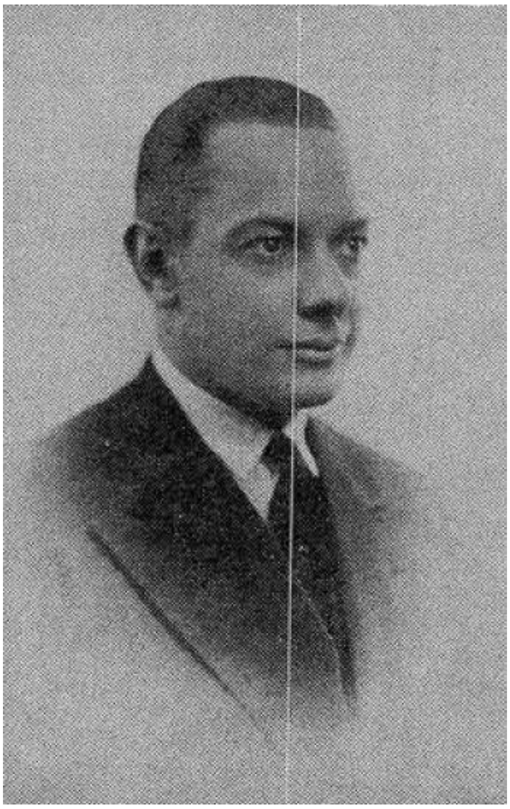

Figure 6. Everard Blanchard. Photograph from Pirán (1972).

Our next Dipterist is the renowned Dr. Raúl Cortés from Chile. From his first article on tachinids from 1944 "Sinópsis histórica de los estúdios sobre Taquínidos Chilenos (Dipt., Tachinidae)" though his last article "Nuevas sinonimias de taquinidos chilenos (Diptera: Tachinidae)" from 1992[34], he completed 48 years of study of Tachinidae. Cortés had a very productive career that put the knowledge of Chilean tachinids to a level never reached for another region of the South America. Graduated as Agricultural Engineer by the University of Chile (1940), he developed an interest on the biological and taxonomic aspects of tachinids because these insects are well known for being important for the biological control, thus this intersection in research lead him to study the Tachinidae (Artigas, 2013). Cortés was a teacher at the Universidad de Chile

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[34] Cortés last contribution to tachinidology was a brief note about a case of multiparasitism in *Euphorocera* Townsend (Cortés, 1993).

(Santiago), Católica de Valparaíso, del Norte (Arica) and Metropolitana de Ciencias de la Educación, in which he advised various entomologists and had done important agricultural research (Coscarón, 2002).

The dexiines from Chile and South Argentina were extensively studied by him. From the 29 new genera of Tachinidae described by Cortés, the first one was the voriine *Dischotrichia* Cortés, 1944, in which its species, *D. caelibata* Cortés, 1944, was described from Valparaiso (Chile). A few years later, he published the Tachinidae part (Cortés, 1946) of the "Catálogo de los Dípteros de Chile" (Stuardo, 1946), an actualization of the older catalogue published in 1889 (Reed, 1888)[35]. Along his active years, he described five new genera of Dexiinae, all valid to this day, in addition to 10 new species, that are all valid and placed in their original genus. Hence, it is clear the great knowledge and work done by Cortés while studying these taxa. A clear advancement that he had, contrasting with Brèthes and Blanchard, was the knowledge of various Chilean tachinids types from foreign museums. As stated by him (Cortés, 1963), in the year of 1957 he could visit the National Museum of Natural History, USA (types of Aldrich and Townsend), the Natural History Museum-UK (types of Walker and Walker) and the Muséum National d'Histoire Naturelle, France (types of Macquart). In addition, he developed a close communication with the late Curtis W. Sabrosky (USNM) during the many years of his studies, assisting him by identifying or comparing material with types in Washington (Cortés, 1986). As a result, his taxonomy was of the greatest quality. Two examples can show this clearly: his "Taquínidos de Tarapaeá y Antofagasta" (Cortés & Campos, 1971) and "Taquinidos de Aysén (XI Región) y Magallanes (XII Región) Chile" (Cortés, 1986). His first work dealt with the knowledge of the Tachinidae of the Chilean desert that corresponds to the provinces of Tarapacá and Antofagasta; he gave new distribution information, elaborated workable keys for all the taxa found in this region and described some new species and genera. His later work dealt with from the world's Southernmost tachinids from the austral territories of Aysen and Magallanes in South Chile, the southern end of the Neotropical Region (or Andean region). In all of these works Córtes provided information about morphology, distribution, taxonomy, the collector and any host record available for those Chilean Tachinidae.

One of the greatest contributions for the dexiines was his dealing with the Dexiini from the Chile and South Argentina, namely: *Dasyuromyia*, *Hyadesimyia*, *Morphodexia*, *Pelycops*, *Notodytes*, that form a peculiar group because of their unique morphology within Dexiini, i.e., arista bare and very robust body. Cortés, as a recognition of his efforts and great accomplishments on

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[35] This was the second older catalogue of Diptera from South America (Amorim & Papavero, 2007).

tachinids from Chile, had four species in his honor: *Dasyuromyia cortesi* Gramajo, 2011, *Cyrtophleba cortesi* (Caltagirone, 1966), *Chaetocnephalia cortesi* González in González & Vergés, 2004 and *Leschenaultia cortesi* Toma & Guimarães, 2002. Finally, by the invitation of Drs. Nelson Papavero and José Henrique Guimarães from the Museum of Zoology of the University of São Paulo, Brazil (two great names of the Brazilian Dipterology), Cortés, in two opportunities (in 1979 and in 1983), came to work and identify the Chilean and Argentine Taquinidae in the museum's collection (Cortés, 1986). To end this survey, the same José Henrique Guimarães will be discussed and his contribution for the Neotropical dexiines will be scrutinized.

Figure 7. Photograph of Raúl Córtes. Kindly shared by Dr. Christian R. González, former student of Córtes.

The last name to be treated in this essay is José Henrique Guimarães, one of the greatest dipterists from Brazil and considered as a worldwide authority on the Neotropical Tachinidae. Throughout his career, from his first article “Contribuição ao conhecimento do gênero *Archytas* Jaennicke, 1867 (Diptera, Tachinidae).” (Guimarães, 1960), until his last one “Redescrição de *Chrysotachina* Brauer & Bergenstamm, 1889 (Diptera, Tachinidae) e redescrição de seis espécies novas das Américas Central e do Sul” (Nunez et al., 2002), he consolidated 42 years of experience as a reference with tachinids. He undergraduate in Veterinary Doctor at formerly Universidade Rural do Brasil (current Universidade Federal Rural do Rio de Janeiro) in Rio De Janeiro in 1962, Master of Sciences in Entomology at the University of California (USA) in 1969 and P.hD in Sciences (Zoology) at the Universidade de São Paulo, in 1973. Since his undergraduate studies[36], he showed great promise in his earlier taxonomic publications of tachinids; for instance, the "contributions to the knowledge of *Archytas* Jaennicke, 1867" published in five parts in three years. This promise could be fulfilled as Guimarães was admitted as a biologist in the then Department of Zoology of the Secretary of Agriculture of the State of São Paulo (current Museum of Zoology of the University of São Paulo - MZUSP). In the year 1966-1967, he received a grant from the "John Simon Guggenheim Memorial Foundation", for research in Diptera at the Systematic Entomology Laboratory, USDA, Washington, DC, under the guidance of Dr. Curtis W. Sabrosky. There, he studed the types of Townsend and the notes of the dipterists (mainly Aldrich and Sabrosky) who were acknowledge with tachinid types from other museums around the world, e.g., Aldrich notes on the occasion of his visit to the Natural History Museum-UK. At the same epoch he started the project "A Catalog of Diptera of Americas, South of the United States", that resulted, in addition to other contributions, with the publication of the Neotropical catalogue of Tachinidae (Guimarães, 1971) and later, with the host and parasite catalogue for the South American Tachinidae (Guimarães, 1977b). This catalogue was the first ever published for the entire Neotropical Region, and it took almost 20 years to be concluded (Papavero 1966-1984). The formidable task delegated to Guimarães, initiated in 1966 and published in 1971, resulting in an incredible number of 2.864 species in 944 genera; Guimarães (1971: 1) himself wrote that: "The family Tachinidae is one of the largest, most difficult, and the most challenging of the families of the Oestroidea complex." In face of long date taxonomic confusion (mainly the ones created to Townsend), he chooses to place the species accordingly to Townsend, and with the modification given by the authors of the catalogue of the Neartic Diptera (Sabrosky & Arnaud, 1965). Córtes (1973b: 260) published a revision of Guimarães' work, and while stating that: "... catalogar los Taquínidos neotropicales lleva en sí el carácter de frustración y desaliento de una empresa que casi con seguridad no dejará a nadie satisfecho." […cataloging the Neotropical Tachinidae carries with it the character of frustration and discouragement of a company that will almost certainly leave no one satisfied.], later, he praised Guimarães (Córtes, 1973b: 260): "El catálogo del Dr. Guimarães es, sin embargo, um esfuerzo encomiable y meritorio, y una útilísima herramienta para todos quienes en el Hemisferio Americano están dedicados o deseen dedicarse al estudio y taxonomía de este apasionante grupo de moscas multiformes, y por eso todos debemos estar reconocidos por tan importante aporte." [The catalogue

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[36] He was advised by Dr. Hugo de Souza Lopes, a renowned scientist that worked mainly with Sarcophagidae, at the Instituto Oswaldo Cruz in Rio de Janeiro state.

of Dr. Guimarães is, however, a commendable and meritorious effort, and a very useful tool for all those in the American Hemisphere who are dedicated or wish to dedicate themselves to the study and taxonomy of this fascinating group of multiform flies, and for that reason we all must recognize such an important contribution.]

His contribution to the knowledge of Neotropical Dexiinae can be compared to the greatest Dipterists that worked in this fauna, like Córtes, Townsend and Aldrich, however, opposingly to Townsend, his efforts were directed to developing revisions of genera and tribes. He revised the dexiine genera *Trichodura* Macquart (Guimarães, 1972) and *Paratheresia* Townsend (Guimarães, 1977c) (= *Billaea*); the tribes Oestrophasiini (Guimarães, 1977a), Uramyini (Guimarães, 1980) and Sophiini (Guimarães, 1982); and finally, he described the following new genera: *Aldrichiopa* Guimarães, 1971, *Neozelia* Guimarães, 1975, *Thelairaporia* Guimarães, 1980, *Neosophia* Guimarães, 1982 and *Sophiella* Guimarães, 1982. In total, Guimarães described 11 genera and 149 species of Tachinidae, of which 5 genera and 30 species (all valid) belong to Dexiinae. As a natural consequence, the first dexiine described by a Brazilian author was made by Guimarães. These species were a directed result of the revision of *Trichodura*: *T. amazonensis* Guimarães, 1972, *T. friburguensis* Guimarães, 1972, *T. longicauda* Guimarães, 1972, *T. sabroskyi* Guimarães, 1972, *T. townsendi* Guimarães, 1972.

Later, Guimarães transferred to the Department of Parasitology (USP). In this institution he developed studies in the areas of Urban Entomology and Veterinary Entomology, retiring in 1993 to, a few years later, returning to MZUSP, where he continued his research, curation and supervision activities (Lamas et al., 2008). Guimarães legacy will remain intact, as those groups and genera reviewed by him are the tachinids more prone for studies of evolution and the most indicated to further develop their potential as biological control, as they are readily recognized and all their names and identity are clear and resolved. For instance, *Diatraea* spp. (Lepidoptera) are considered the most important pest in sugarcane in Colombia, and one of the tachinids used for their biological control is *Billaea claripalis* (Bustillo, 2013); for the identification of this species the revision of Guimarães (1977c) for *Paratheresia* (= *Billaea*) with its keys and descriptions, is extensively used to his day. After the reestablishing the tribe Oestrophasiini (Guimarães, 1971), and revising all their genera and species (Guimarães, 1977a), it was possible to state that the presence of microtype eggs is the most distinguished trait of this group, putting them as a separate tribe from Dufouriini (Santis &Nihei, in prep). As a recognition of the importance of the work of Guimarães, he had, until now, five species named after him: *Eucelatoria guimaraesi* Sabrosky, 1981, *Thysanopsis guimai* Toma, 2001, *Neosophia guimaraesi* de Santis & Nihei, 2019, *Zelia guimaraesi* Dios & de Santis, 2019 and

Ormiophasia guimaraesi Gudin & Nihei, 2019. It is important to note that the last three species named for him were done by new Brazilian authors that are working with Neotropical Tachinidae and are collecting all the fruits given by Guimarães, that gave a solid ground and space for the new generation of tachinidologists to work with these insects at the Neotropics.

Figure 8. Photograph of José Guimarães in his one-year (1966-1967) fellowship at the Systematic Entomology Laboratory, USDA (USA). Available at: https://www.gf.org/fellows/all-fellows/jose-henrique-guimaraes/

Finally, a note about the type localities given by Guimarães will be shortly discussed. From six species of dexiine described by him, the type locality Muri, a city of Nova Friburgo, is quoted. This place reflects the collections that he and his wife, Gred Girid Koster Mueller Guimarães, carried out by them at the Muri district, in the mountain region of the state of Rio de Janeiro (Lamas et al., 2008). Another type locality frequently seen by consulting Guimarães's works is Nova Teutônia, from Santa Catarina state, all of them collected by a single person: Fritz Plaumann. A few bibliographical notes will be given herein in order to appreciate the importance of this German born and self-taught entomologist and naturalist that collected in Brazil for more than 60 years and sold parts of his collection to museums at Brazil and abroad.

Fritz Plaumann (1902-1994) was a German immigrant who arrived in Brazil, with his family, in 1924 and settled in the then German colony of Nova Teutônia located in the western region of Santa Catarina, today in the district of Nova Teutônia, city of Seara in Santa Catarina state (Lubenow, 2016). The practice of collecting was Fritz Plaumann's main source of income throughout his life, and this lead the intense commercialization of specimens and other biological materials for scientist and museums around the world (Lubenow, 2016). The majority of his collections were made by the district of Nova Teutônia, at the Alto Uruguai Catarinense a semidecidual stational forest of west Santa Catarina. He was, thus, mainly from that time, a collector in an isolated area, who lived in the small German colony of Nova Teutônia, surrounded by the forest of the Santa Catarina backlands, an inhospitable, distant place, far from civilization. However, he was always in permanent contact with several researchers, entomologists, zoologists and scientific institutions (Lubenow, 2016).

Plaumann always searched for untouched forests to collect for his scientific collections. He knew that he would find many rarities in the closed forests that had not yet been affected by agricultural modernization and deforestation. He maintained the initiative and willing to work on behalf of Brazilian fauna and increase the regional collection to be used by other scientists today and in the future (Plaumann *in* Spessato, 2001). Thus, even with many difficulties in obtaining the literature and work materials, and far from urban and scientific centers (Lubenow, 2016), Plaumann managed to form a collection of significant relevance for various areas of knowledge. He was also aware of the quality and rarity that these insects needed to be in order to be used by scientists, and this can be seen in the following quote from his diaries (Plaumann *in* Spessato, 2001: 99): "Muito dependia, naturalmente, também do bom estado do material enviado. Na ciência a avaliação do material não depende do tamanho do objeto, mas sim da raridade. Em se tratando de espécies novas, antes desconhecidas e não descritas, tais espécies existiam há muito tempo, porém não foram encontradas e registradas cientificamente." [Much, of course, also depended on the good condition of the material sent. In science, the evaluation of the material does not depend on the size of the object, but rather on the rarity. In the case of new species, previously unknown and not described, these species have existed for a long time, but they were not found and scientifically registered.]

However, in 1967, the Law on the protection of fauna, which restricted the act of collecting specimens came into force in Brazil. Over the following years, Plaumann had many problems in obtaining authorization to collect insects and send remittances abroad (Lubenow, 2016). This, in addition to his old age, lead Fritz Plaumann to sell his collection to the Municipality of Seara in 1982, culminating in the foundation of the "The Fritz Plaumann Entomological Museum" in the same year. The construction ended in 1988 when the museum was finally opened. He continued to work on expanding the collection, in addition to being hired by Seara City Hall to be responsible for the museum (Lubenow, 2016). The collector and the collection were only separated by Plaumann's death in 1994. According to Souza (1998), the museum contains a collection with more than 73,036 specimens and 9,601 species, which represent 19 insect orders, 318 families and 2,219 genera. Furthermore, Diptera is represented by 218 identified species, being mostly represented by Stratiomydae (125), Asilidae (85), Tabanidae (61) and Sarcophagidae (30) (Souza, 1998). A very important fact is that of the 73,036 specimens, 55% are determined only up to family, and in relation to Diptera, there are 2.215 undetermined specimens in that collection (Souza, 1998). In the face of this information, and the fact that in various museums that Plaumann sold his collections, there are plenty of undetermined material[37], I wonder what remains to be discovered in this material, that Plaumann dedicated all life, and was collected with so much care and passion. Keen observer, great naturalist and a careful collector, his work, as a consequence, represents one of the most detailed inventories of the local insect fauna ever carried out in the Neotropical region (Silva, 1998). As a proof of his influence, Plaumann was named after three species of Dexiinae by Guimarães, *Billaea plaumanni* (Guimarães, 1977), *Euoestrophasia plaumanni* Guimarães, 1977, *Uramya plaumanni* Guimarães, 1980; in addition to three more species found in other groups in Tachinidae. In total, Plaumann had 77 species in Diptera named in his honour for acknowledgement of his work. Furthermore, he received the highest award in the field of science in Germany: the Grand Cross of Scientific Merit.

To end this limited and brief historical overview of Dexiinae at the Neotropics, I think it is appropriate to quote the views and passion of Fritz Plaumann, as this is, was, and will be, the motive behind all entomological studies. The following excerpt came from the message written by Plaumann and read publicly at the Museum's opening ceremony: “Que meu trabalho entomológico possa contribuir para incentivar a admiração e o amor à natureza e estimular a reflexão sobre a mesma”. [May my entomological work contribute to encourage admiration and love for nature and stimulate reflection on it.]

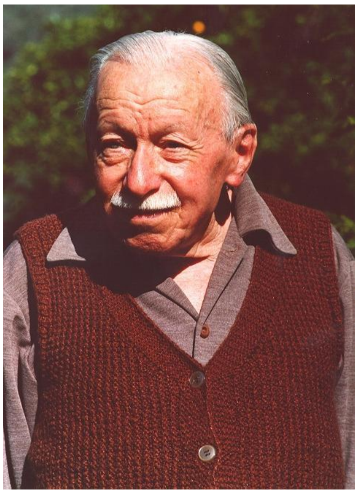

Figure 9. An old Fritz Plaumann. Available at: http://www.museufritzplaumann.ufsc.br/galeria_fotos/photos/042.html

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[37] Even with eight type localities given by Guimarães's work with Neotropical Dexiinae, there are some hundreds of underdetermined materials of Tachinidae collected by Plaumann at MZSP.

Figure 10. A young Fritz Plaumann in the woods of Alto Uruguai Catarinense, collecting insects. Photograph from the 1930s. Source: Fritz Plaumann House.

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