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**Sistemática e evolução das aranhas orbitelas
do gênero *Wagneriana* F.O. Pickard-Cambridge,
1904 (Araneae: Araneidae)**

**Systematics and evolution of the orb-weaving
spider genus *Wagneriana* F.O. Pickard-
Cambridge, 1904 (Araneae: Araneidae)**

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RESUMO

Embora vários gêneros neotropicais da família Araneidae tenham sido revisados usando padrões taxonômicos modernos, as filogenias ao nível de espécie e as relações filogenéticas entre os gêneros ainda são pouco conhecidas. Este estudo foi delineado para testar o monofiletismo do gênero neotropical *Wagneriana* F. O. Pickard-Cambridge, 1904 e sua posição filogenética, através de uma análise de evidência total. A matriz combinada incluiu 167 caracteres fenotípicos e aproximadamente 4.800 pares de bases gerados para três *loci* mitocondriais e seis nucleares. O conjunto de dados consiste em 82 terminais representando 100% da diversidade descrita do gênero *Wagneriana* (37 espécies após alterações taxonômicas) mais cinco espécies não descritas e 33 terminais do grupo externo representando 31 espécies. Para avaliar o significado filogenético da evidência fenotípica, comparações entre análises de evidência total e análises exclusivamente moleculares foram realizadas. Além disso, para avaliar o efeito dos critérios de alinhamento e otimalidade, foram realizadas múltiplas abordagens analíticas utilizando os programas POY, TNT, RAxML, GARLI, IQtree e MrBayes. Em geral, os resultados obtidos nas diferentes abordagens mostraram congruência. Em todos os casos, *W. carimagua* Levi, 1991 e *W. uropygialis* Levi, 1991 foram aninhados dentro dos gêneros *Parawixia* F. O. Pickard-Cambridge, 1904 e *Alpaida* O. Pickard-Cambridge, 1889, respectivamente, e as espécies nominais remanescentes do gênero *Wagneriana* foram obtidas em três clados principais, nenhum dos quais formou um par de táxons irmãos. No entanto, as relações de grupo-irmão dos principais clados, bem como suas relações internas, foram fortemente influenciadas pela abordagem analítica empregada. A escolha dos critérios de alinhamento teve efeitos topológicos comparáveis aos dos critérios de otimalidade. Dentro do contexto de máxima verossimilhança, a escolha do programa afetou a maximização do score de verossimilhança e a topologia. Embora a evidência fenotípica compreendesse apenas 2,80-3,05% das matrizes de evidencia total, teve impacto nos valores de suporte e na topologia. Em geral, a inclusão de evidências fenotípicas, independentemente do critério de otimalidade usado, aumentou os valores de suporte de vários clados do grupo interno e externo. Além disso, o monofiletismo de vários clados só foi recuperado com a adição de caracteres fenotípicos. De acordo com os resultados filogenéticos, um novo gênero de Araneidae é proposto e *Paraverrucosa* Mello-Leitão, 1939 é reestabelecido. Além disso, cinco espécies novas de *Wagneriana* são descritas e descrições complementares para sete espécies são fornecidas. Este estudo apresenta a primeira análise filogenética de evidência total de um gênero neotropical da família Araneidae e discute o impacto da inclusão de evidência fenotípica e a escolha de critérios de alinhamento e otimalidade em análises filogenéticas.

ABSTRACT

Although several Neotropical genera of the family Araneidae were revised using modern taxonomic standards, species-level phylogenies and phylogenetic relationships among genera remains poorly understood. This study was designed to test the monophyly of the Neotropical araneid genus *Wagneriana* F. O. Pickard-Cambridge, 1904 and its phylogenetic placement by conducting a total evidence analysis. The combined matrix included 167 phenotypic characters and approximately 4,800 base pairs generated for three mitochondrial and six nuclear loci. The dataset consists of 82 terminals representing 100% of the described diversity of the genus *Wagneriana* (37 species after taxonomic changes) plus five undescribed species and 33 outgroup terminals of 31 species. To evaluate the phylogenetic significance of the phenotypic evidence, comparisons between total evidence analyses and molecular-only analyses were conducted. In addition, to evaluate the effect of the alignment and optimality criteria, multiple analytical approaches were conducted using the programs POY, TNT, RAxML, GARLI, IQtree and MrBayes. In general, the results obtained across the different approaches showed congruence. In all the cases, *W. carimagua* Levi, 1991 and *W. uropygialis* Levi, 1991 were nested within the genera *Parawixia* F. O. Pickard-Cambridge, 1904 and *Alpaida* O. Pickard-Cambridge, 1889, respectively, and the remaining nominal species of the genus *Wagneriana* fell into three main clades, neither of which formed a pair of sister taxa. However, sister-group relationships of the main clades, as well as, its internal relationships were strongly influenced by the employed analytical approach. The election of alignment criteria had comparable topological effects to that of optimality criteria. Within the maximum likelihood context, the program choice affected the maximization of the likelihood score and the tree topology. Although phenotypic evidence comprised only 2.80-3.05% of the total evidence matrices, it had impact in support values and topology. In general, the inclusion of phenotypic evidence, irrespective of the optimality criterion used, increased the support values of several ingroup and outgroup clades. Furthermore, the monophyly of several clades was only recovered with the addition of phenotypic characters. In accordance with the phylogenetic results, a new araneid genus is proposed and *Paraverrucosa* Mello-Leitão, 1939 is resurrected. Moreover, five *Wagneriana* species are newly described and complementary descriptions for seven species are provided. This study presents the first total evidence phylogenetic analysis of a Neotropical Araneidae genus and discusses the impact of the inclusion of phenotypic evidence and the choice of alignment and optimality criteria in phylogenetic analyses.

1. INTRODUCTION

1.1. Araneae phylogeny

Araneae (spiders) is a megadiverse arthropod clade with 47195 described species distributed among 4073 genera and 113 families (World Spider Catalog, 2018). Spiders are among the most abundant predators in almost every terrestrial ecosystem, having a considerable impact in their prey populations. Nyffeler & Birkhofer (2017) estimates that the annual prey kill of the global spider community is in range of 400-800 million metric tons, being insects their main prey. The monophyly of Araneae is supported by the presence of spinning appendages at the posterior end of the abdomen and by the male pedipalpi modified for sperm transfer (Wheeler *et al.*, 2017). Araneae is one of the few hyperdiverse arthropod orders with a complete online catalog that includes synonymic lists and the associated literature (World Spider Catalog, 2018), facilitating the taxonomical research. In recent years, the remarkable diversity of spider behavior, morphology and ecology, which turns them into excellent research models for several fields of biology (see Penney, 2013), has been studied in an explicit phylogenetic context.

As in numerous arthropods clades, the recent history of spider systematics involves (1) gathering different sources of evidence by means of diverse technological resources, (2) increasing taxon sampling by means of extensive field trips and new fossils discoveries, (3) differentiating plesiomorphies of apomorphies applying Hennigian principles (Hennig, 1966), and finally, (4) establishing monophyletic classifications (Agnarsson *et al.*, 2013; Hormiga & Griswold, 2014; Griswold & Ramírez, 2017). To some extent, the historical path of spider phylogenetic studies also echoes some trends of theoretical discussions within systematics, involving several topics such as the ontological status of character and homology, the merit of the total evidence approach, and the epistemological justification for employing different optimality criteria (see section 1.5).

Cornerstones for the development of spider phylogenetics are the detailed characterization of spinning behavior for some taxa (Eberhard, 1982), the extensive characterization of genitalia and spinnerets spigot morphology using SEM (*e.g.* Hormiga, 2000; Agnarsson, 2004; Griswold *et al.*, 2005; Álvarez-Padilla & Hormiga, 2011; Ramírez, 2014; Lopardo & Hormiga, 2015) and, more recently, micro-CT scanning (*e.g.* Lipke *et al.*, 2014; Michalik & Ramírez, 2014; Huckstorf *et al.*, 2015; Lipke & Michalik, 2015; Lipke *et al.*, 2015; Labarque *et al.*, 2017), the use of DNA data from the so-called usual suspects loci (*e.g.* Gregorič *et al.*, 2015a; Wang *et al.*, 2015; Liu *et al.*, 2016; Dimitrov *et al.*, 2017; Wheeler

et al., 2017), and genome-scale data (Bond *et al.*, 2014; Fernández *et al.*, 2014; Garrison *et al.*, 2016; Hedin *et al.*, 2018).

In their recent synopsis of spider phylogeny, Griswold & Ramírez (2017) present an updated spider tree of life that emphasizes areas of consensus in which multiple analyses, using different sources of evidence, have converged, and areas of instability in which several relations remain highly contentious. According to this hypothesis, Araneae is basally divided in Mesothelae, represented by the southeast Asian Liphistiidae that retains external abdominal segmentation, and Opisthothele in which abdominal segments 12-18 are suppressed and spinnerets appear to be beneath the apex of the abdomen. The latter clade is further divided in two major lineages: Mygalomorphae (tarantulas and their allies, 15 families worldwide with 306 genera and 2473 species, World Spider Catalog, 2018), which has reduced spinning organs with anterior median spinnerets completely absent, and Araneomorphae (the so-called “true spiders”, 98 families worldwide with 3759 genera and 44606 species, World Spider Catalog, 2018), supported by the presence of cribellum and pyriform silk glands. Within Araneomorphae, several monophyletic clades are supported by morphological synapomorphies related in most cases with genitalia morphology. For example, fusion of two or more sperm cells into a single transfer unit for Synspermiata, female genitalic system with separate ducts for copulation and fertilization for Entelegynae, and presence of a retrolateral tibial apophysis in the male palp for the RTA clade (Griswold & Ramírez, 2017).

One of the most outstanding results of recent spider phylogenetic analyses is the non-monophyly of the Entelegynae clade Orbiculariae (Garrison *et al.*, 2016; Dimitrov *et al.*, 2017; Griswold & Ramírez, 2017; Wheeler *et al.*, 2017). Orbiculariae (orb-weaving spiders), traditionally composed by the cribellate Deinopoidea and the ecribellate Araneoidea, was considered for several years an indisputable monophyletic group by the complex suite of stereotypical behaviors used to construct the orb-web. However, new evidence gathered by means of genome-scale data (Bond *et al.*, 2014; Fernández *et al.*, 2014; Garrison *et al.*, 2016) and Sanger-sequencing coupled with enhance taxon sampling (Agnarsson *et al.*, 2013; Dimitrov *et al.*, 2017), led to the hypothesis that orb-webs are an ancient development of a more inclusive group, subsequently modified or lost in several lineages (*e.g.* the speciose RTA clade) (Wheeler *et al.*, 2017; Griswold & Ramírez, 2017). As pointed out by Griswold and Ramírez (2017) this new hypothesis would imply a new approach to web architecture evolution, as new hypothesis of homology would emerge in several clades when considering an ancient orb-weaver ancestor.

Although several Araneomorphae clades seem to be highly corroborated by diverse sources of evidence, numerous lineages remain highly contentious. Therefore, hypothesis about evolution of phenotypic characters as genital morphology and web architecture need to be continuously submitted to rigorous tests with new sources of evidence. An excellent example for this situation are the interfamilial relationships within the orb-weaving superfamily Araneoidea, which have dramatically changed in the last decade (Dimitrov *et al.*, 2017).

1.2 Araneoidea phylogeny

The superfamily Araneoidea currently comprises 12416 described species distributed among 1131 genera and 17 families (Dimitrov *et al.*, 2017; World Spider Catalog, 2018). Araneoidea monophyly is supported by the presence of paracymbium in the male palp and flagelliform and aggregate silk glands (Griswold *et al.*, 1998; Hormiga & Griswold, 2014).

The first comprehensive phylogenetic analysis of the interfamilial relationships within Araneoidea was that of Griswold *et al.* (1998). In this work, 93 phenotypic characters were scored for representatives of 12 Araneoidea families (ingroup) and two Deinopoidea families (outgroup), and parsimony was used as the optimality criterion for hypotheses choice. Griswold *et al.* (1998) recovered a single most parsimonious tree with the family Araneidae as the sister group of the remaining araneoid families, which constituted the so-called “derived araneoids” clade. Within the latter clade, several lineages supported by morphological synapomorphies were recognized: the Tetragnathidae family (tetragnathines, metines and nephilines), the “reduced piriform clade” (symphytognathoids and araneoid sheet web weavers), the “araneoid sheet web weavers” (linyphioids, theridioids, and cyatholipoids), the “spineless femur clade” (theridioids and cyatholipoids) and the cyatholipoids (Cyatholipidae and Synotaxidae). According to Griswold’s *et al.* (1998) optimal hypothesis, the evolution of araneoids involved reduction in overall size, loss of tegular sclerites, reduction in leg spines, simplification of spinning fields and transformation of the plesiomorphic orb web to the araneoid sheet web and subsequently to the gumfoot web.

Ten years after Griswold *et al.* (1998) seminal work, Lopardo & Hormiga (2008) tested the phylogenetic placement of the enigmatic Tasmanian genus *Acrobleps* Hickman, 1979 within Araneoidea adding six new terminals and two morphological characters to Griswold’s *et al.* (1998) matrix. After the addition of this new evidence, some of the lineages within the so-called reduced piriform clade were not recovered (*i.e.* araneoid sheet web weaver, spineless femur clade and cyatholipoids) and new monophyletic clades were obtained such as the so-

called “clawless female clade” which included Synsphyridae, Cyatholipidae and symphytognathoids. In addition, a new scenario for web evolution was proposed suggesting a double origin of the orb web. Nevertheless, Lopardo & Hormiga (2008) cautioned that their taxon sample was insufficient to significantly advance the hypothesis of Griswold *et al.* (1998), and as such, they succinctly stated that “any rigorous attempt to resolve araneoid interfamilial relationships will require a dense taxonomic sample and multiple lines of empirical evidence”.

In their monographic work of the family Micropholcommatidae (now considered as a subgroup of Anapidae), Rix & Harvey (2010) reanalyzed Griswold’s *et al.* (1998) and Lopardo & Hormiga’s (2008) matrices, including six new taxa, one new morphological character and three character modifications. These authors recovered a monophyletic Micropholcommatidae which together with Anapidae, Symphytognathidae and “teutoniellids” constituted the newly named “enlarged basal cylindrical gland” clade. Interfamilial relationships within Araneoidea were obtained as poorly resolved. As Lopardo & Hormiga (2008), Rix & Harvey (2010) also underscored that future phylogenetic work should increase the taxon sampling, especially focusing in the family Anapidae, which they considered crucial to resolve the phylogeny of the symphytognathidan clade within Araneoidea (see also Schütt, 2003).

Dimitrov *et al.* (2012) were the first researchers to considerably expand the taxon sampling of Griswold’s *et al.* (1998) analysis. These authors aimed to test the monophyly of the clade Orbiculariae using molecular evidence from six markers and a sample of 50 spider families, 19 of which were araneoid families. Dimitrov *et al.* (2012) analyzed their data with multiple optimality criteria and provided the first empirical support for the monophyly of Orbiculariae (Deinopoidea, Araneoidea and Nicodamidae) based exclusively in molecular data. In addition, their character optimization suggested the plesiomorphic character of the typical geometric orb web and multiple independent transitions from orbs to diverse web architectures. Dimitrov *et al.* (2012) recovered Araneoidea as a well-supported clade but most interfamilial relationships were considered as poorly resolved due to low bootstrap support values. Moreover, Mysmenidae, Theridiosomatidae and Anapidae were not recovered as monophyletic families.

All the previously mentioned results were synthesized by Hormiga & Griswold (2014) who presented a summary cladogram for Araneoidea where most of the interfamilial relationships among araneoids are unresolved. Hormiga & Griswold (2014) concluded that future efforts to elucidate the interfamilial relationships within Araneoidea should include the description of the remaining orbicularian diversity coupled with a proper documentation of natural history traits, and the use of genomic-scale data.

Finally, Dimitrov *et al.* (2017) proposed the most comprehensive phylogenetic hypothesis for Araneoidea to date, including representatives of all the known families of the clade (see also Wheeler *et al.*, 2017). In this analysis, based solely on Sanger-sequencing molecular evidence, most of the araneoid families were recovered as highly supported clades (ML bootstrap values > 70, posterior probabilities > 95 and maximum parsimony bootstrap > 70), whereas the nodal support for interfamilial relationships was in general low, except in the clades Mimetidae plus Arkyidae + Tetragnathidae and Malkaridae plus Paraarchaeidae. Nicodamoidea was recovered as the sister group of Araneoidea and Orbiculariae was not recovered as a monophyletic group. Some of the most important taxonomic changes in accordance with the preferred phylogenetic hypothesis were the establishment of two new family ranks (*i.e.* Physoglenidae and Arkyidae), the classification of Nephilinae as a subfamily of Araneidae and the recognition of three family-level synonymies. According with Dimitrov's *et al.* (2017) character optimization, the orb web is plesiomorphic and there have been independent origins of the cobweb and the stereotyped aerial sheet web, as well as independent losses of the foraging web within Araneoidea.

Dimitrov's *et al.* (2017) results are based on the largest sample of araneoids analyzed to date, and as such, represents the most severe test of Araneoidea monophyly. However, considering the vast diversity of this spider clade, new topological changes and the concomitantly alterations in character optimization should be expected in the light of new evidence (terminals and characters). In addition, it should be noticed that despite several efforts in the last decades (see Hormiga (1993, 1994a) for Pimoidae; Hormiga (1994b, 2000), Miller & Hormiga (2004), Arnedo *et al.* (2009) and Wang *et al.* (2015) for Linyphiidae; Agnarsson (2004), Arnedo *et al.* (2004) and Liu *et al.* (2016) for Theridiidae; Hormiga *et al.* (1995) and Álvarez-Padilla & Hormiga (2011) for Tetragnathidae; Benavides *et al.* (2017) for Mimetidae; Schütt (2003), Rix & Harvey (2010) and Lopardo & Hormiga (2015) for symphytognathoids and Scharff & Coddington (1997), Kuntner *et al.* (2013), Cheng & Kuntner (2014) and Gregorič *et al.* (2015a) for Araneidae), the phylogenetic relationships within some araneoid families remain in general poorly understood. The family Araneidae, which includes some of the most intensively studied genera of spiders, is paradoxically one of the most critical examples of this situation.

1.3 Araneidae phylogeny

Araneidae is one of the most diverse spider families currently including 3125 species in 173 genera (World Spider Catalog, 2018). Araneids occur in all continents except the polar

regions, and are abundant and diverse in the Neotropical region (Pinzón *et al.* 2010; Santos *et al.*, 2017), which concentrates ca. 40% of its known richness. Defining morphological characters for the delimitation of Araneidae has been challenging due to its huge morphological, ecological and behavioral diversity. Dimitrov *et al.* (2017) listed the presence of sustentaculum on the tip of the fourth tarsi, the presence of radix in the embolic division of the male palp and the presence of nonbirefringent cement at all SS-line and radius junctions as putative synapomorphies for araneids.

The taxonomy and morphology of the family Araneidae are well-studied in relation to the remaining araneoid families, due mostly to H.W. Levi's monographic revisions which included detailed illustrations of somatic and genital morphology in a standardized fashion (see the complete list of Levi's publications in Leibensperger, 2016). However, the monophyly of most araneid genera has not been tested and the phylogenetic relationships among them remain highly contentious (Kuntner *et al.* 2013; Hormiga & Griswold 2014; Dimitrov *et al.*, 2017; Wheeler *et al.*, 2017). In the following paragraphs, I present a synthetic revision of the phylogenetic work within the family Araneidae and I also highlight the current challenges for the phylogenetic understanding of its diversity.

Since 1968, H.W. Levi conducted a series of monographic works for several Araneidae genera establishing high-quality standards for Araneae taxonomy in general and Araneidae taxonomy in particular. In some of these monographs, Levi included comparative morphological tables highlighting similarities and differences among supposedly related genera and also included putative synapomorphies in genera diagnoses. Some of these putative synapomorphies were mapped by Levi & Coddington (1983, see also Levi, 1983) in a tree diagram of Araneidae genera relationships. In this tree, the rotation of the bulb within the cymbium of the male palpus was indicated as a synapomorphy of Araneidae, and within the family, putative synapomorphies related with the male palp morphology (as anticipated by Levi, 1978a), eyes morphology and arrangement and web architecture were used to delineate several groups.

Nevertheless, despite his high-quality standards for taxonomy and his unparalleled knowledge of Araneidae comparative morphology, Levi was rather reluctant to conduct phylogenetic analyses among and within Araneidae genera as he considered crucial to first conduct the taxonomic revision of each genus (see Levi, 1992a p. 2 and Levi, 1995a p. 154). Unfortunately, by the late nineties only about a third of Araneidae genera had been revised and as pointed out by Scharff & Coddington's (1997), taken literally Levi's suggestion would postpone phylogenetic studies of Araneidae several centuries.

In 1997 Scharff & Coddington published the most taxon-rich phylogenetic analysis among araneid genera to date, including 70 genera (57 araneids) and 82 phenotypic characters. As highlighted by these authors, due to the immense diversity of Araneidae their objective was not to analyze the phylogeny of all araneid genera, but rather to infer the basic phylogenetic structure of the family. Scharff & Coddington's (1997) ingroup taxonomic sampling was designed to represent most of Simon's (1892-1895) Araneidae classification which until then remained the most comprehensive treatment of the family. Parsimony was used as optimality criterion for hypothesis choice and the preferred working hypothesis was selected after eliminating trees containing zero-length branches, discriminating among most parsimonious trees with successive character weighting and selecting topologies that maximized homology rather than convergence in complex characters.

Scharff & Coddington's (1997) working hypothesis recovered Araneidae as a monophyletic family further divided into two major lineages: the Argiopoid clade (including representatives of the subfamilies Cyrtophorinae, Argiopinae, Gasteracanthinae, Micratheninae, and Cyrtarachninae) and the subfamily Araneinae. Several genital and sexual characters such as the radix, distal hematodocha, subterminal apophysis, endite tooth and terminal apophysis contributed to the delimitation of internal clades within these two major lineages. These characters were in general compatible, nested one within the other and were congruent with other characters. Conversely, high levels of homoplasy were detected for the conductor lobe, paramedian apophysis, stipes and embolus cap.

Scharff & Coddington (1997) stressed that their matrix was and remains sensitive to inclusion or exclusion of characters and taxa due to the low characters/terminals ratio. For example, they reported to have obtained 60,000 most parsimonious trees after analyzing earlier versions of their data matrix. They also highlighted several regions of their preferred tree with high cladistic instability. In particular, they emphasized the case of the subfamily Araneinae and suggested that further detailed coding of genital characters coupled with the inclusion of additional terminals within this clade, would be crucial to make greater progress in unraveling the phylogenetic relationships among its genera. Finally, after an overview of the consistency between different classes of characters by plotting the consistency index, retention index and characters' weights after successive weighting, Scharff & Coddington (1997) reported behavior, spinnerets and female genitalia as being the more concordant character systems and male genitalia, appendages and prosomal features as the least concordant. Scharff & Coddington (1997) concluded that future work in Araneidae phylogeny should focus on

refining homology hypotheses, searching for new characters and making the data matrix more representative of araneid diversity.

Levi (1999) criticized some of Scharff & Coddington's (1997) characters, considering them as poor phylogenetic characters for being highly homoplastic (*e.g.* absence or presence of scape and stipes and scape texture) or size-correlated (*e.g.* coxae I hook, femur II groove). In addition, Levi (1999) criticized Scharff & Coddington's (1997) decision of keeping the conductor lobe and the paramedian apophysis as separate characters (see also Levi, 2001, p. 450). Finally, Levi (1999) commented in relation with Scharff & Coddington's (1997) work that 'The many homoplasies and later losses of characters used in their present cladogram are disconcerting. The publication states that the palpi were not very useful for the study of phylogeny. One wonders if the examination of several species of each genus would have prevented these errors'. In general, Levi's critique highlights aspects that Scharff & Coddington (1997) recognized as future improvements of their phylogenetic approach.

Scharff & Coddington's (1997) phenotypic matrix was the basis for assessing the phylogenetic position of several araneid genera from Africa, Asia and Australia (Tanikawa, 2000 – *Zilla* C. L. Koch, 1834; Kuntner, 2002 – *Perilla* Thorell, 1895; Kuntner & Hormiga, 2002 – *Syngafrotypa* Benoit, 1962; Smith, 2005 – *Cyphalonotus* Simon, 1895, *Ideocaira* Simon, 1903, *Micropoltys* Kulczyński, 1911 and *Poltys* C. L. Koch, 1843; Harmer & Framenau, 2008 – *Telaprocera* Harmer & Framenau, 2008; Schmidt & Scharff, 2008 – *Acusilas* Simon, 1895; Framenau *et al.*, 2010a – *Demadiana* Strand, 1929, now included in the Family Arkyidae; Framenau *et al.*, 2010b – *Backobourkia* Framenau, Dupérré, Blackledge & Vink, 2010; Framenau, 2011 – *Lariniophora* Framenau, 2011; Joseph & Framenau, 2012 – *Plebs* Joseph & Framenau, 2012). Tanikawa (2000), Kuntner (2002), Kuntner & Hormiga (2002) and Smith (2005) coded their focal species for the 82 phenotypic characters of Scharff & Coddington (1997) without adding additional characters. Harmer & Framenau (2008), Framenau *et al.* (2010b) and Framenau (2011) used the same latter approach but updating the coding for terminals of the subfamily Nephilinae following Kuntner (2006, 2007) and Kuntner *et al.* (2008); Framenau *et al.* (2010b) also coded a new phenotypic character. Schmidt & Scharff (2008) and Framenau *et al.* (2010a) employed Scharff & Coddington's (1997) matrix to test the generic placement of their focal group and after this preliminary result, they selected an outgroup for a more detailed analysis of species-level relationships using new characters; Framenau *et al.* (2010a) also updated the coding for terminals of the subfamily Nephilinae. Finally, Joseph & Framenau (2012), considering previous results in which Australian genera with paramedian apophysis always fall in the same region of Scharff & Coddington's (1997)

tree, did not add their terminals to Scharff & Coddington's (1997) matrix. Instead, they used Scharff & Coddington's (1997) preferred tree to select some outgroup terminals and coded 35 phenotypic characters to propose a species-level phylogenetic hypothesis for the genus *Plebs*. Recently, Gregorič *et al.* (2015b) presented a species-level phylogenetic hypothesis for the African genus *Caerostris* Thorell, 1868. In this work, only molecular data (two markers) were used as evidence to infer the phylogenetic relationships.

In the case of Nearctic and Neotropical lineages, only the genera *Chaetacis* Simon, 1895, *Eustala* Simon, 1895 and *Micrathena* Sundevall, 1833 have been submitted to phylogenetic analyses (Magalhães & Santos, 2012; McHugh *et al.*, 2014; Poeta *et al.*, 2017). Magalhães & Santos, (2012) coded 146 phenotypic characters for 51 terminals to test the monophyly of *Micrathena* and *Chaetacis* and their phylogenetic placement. The authors proposed *Chaetacis* as a junior synonym of *Micrathena*, diagnosed twelve species groups within *Micrathena* and recovered the so-called Gasteracanthoid clade or the genus *Cyclosa* Menge, 1866, depending on the optimality criterion used, as sister groups of *Micrathena*. McHugh *et al.* (2014) presented a molecular-based phylogenetic analysis of Caribbean *Micrathena* species employing three molecular markers and a limited sample of outgroups. Finally, Poeta *et al.* (2017) coded 179 phenotypic characters for 108 terminals to test the monophyly and phylogenetic position of the speciose genus *Eustala*. These authors corroborated the monophyly of *Eustala* and recovered *Metazygia* F.O. Pickard-Cambridge, 1904 as its sister group.

The study by Scharff & Coddington (1997) remains the most taxon-rich investigation into the relationships among araneid genera to date, and as such, the more severe test of the family monophyly and the relationships among its genera. Nevertheless, three recent works have greatly improved the taxon sampling of some lineages within Araneidae. Kuntner *et al.* (2013), based on molecular evidence from eight molecular markers and 231 phenotypic characters, presented the most taxon-rich phylogenetic hypothesis for the subfamily Nephilinae to date. In this work, a sample of 28 out of 40 Nephilinae species was used and a total evidence analysis under different optimality criteria was conducted. Nephilinae was recovered as a monophyletic lineage, a new genus was proposed and the phylogenetic affinities of nephilines within Araneoidea were considered as ambiguous due to low support values. Cheng & Kuntner (2014) investigated the macroevolutionary patterns of sexual size dimorphism in the subfamily Argiopinae by means of a molecular-based phylogeny. These authors sampled 47 ingroup species (approximately 50% of the described diversity for the subfamily) and 16 outgroups and analyzed sequences from four molecular markers. Argiopinae was recovered as a well-

supported monophyletic group and *Cyrtophora* Simon, 1864 was recovered as its sister group. Finally, Gregorič *et al.* (2015a), using molecular evidence from six markers for 112 orbicularian exemplars, proposed a phylogenetic hypothesis for the subfamily Zygiellinae. Their results recovered Nephilinae as the most basal lineage within Araneidae, followed by a well-supported Zygiellinae and the remaining araneids.

Currently, a team of arachnologists are conducting an updated phylogenetic analysis for the family Araneidae employing molecular and morphological evidence (see Joseph & Framenau, 2012, p. 279-280). This unpublished work includes an augmented taxon sample of the major Araneidae lineages previously recognized by Scharff & Coddington (1997). One of the major preliminary results of this ongoing analysis is that the speciose Araneinae subfamily is not monophyletic (see Joseph & Framenau 2012, p. 279). These findings corroborate the importance of incrementing the amount of evidence (characters and terminals) for testing phylogenetic hypotheses within Araneidae and also highlights that Araneinae is one of the lineages that deserves additional attention in future works. Moreover, as stressed above, after Scharff & Coddington (1997) seminal work, most of the research efforts have been focused in studying African, Asian and Australian araneid genera, leaving behind lineages distributed across the Neotropical region which concentrates approximately 40% of the diversity of the family. Also, despite the remarkable morphological knowledge of Araneidae, as commented earlier in this section, no phylogenetic analysis based on both molecular and morphological evidence has been published so far for a Neotropical Araneidae lineage.

In the following section I present a synthetic revision of the taxonomic history of the Neotropical Araneinae genus *Wagneriana* F. O. Pickard-Cambridge, 1904 and I mention several aspects that turn the phylogenetic research within the genus a highly relevant endeavor considering the *status quo* of Araneidae systematics.

1.4 The Neotropical orb-weaving spider genus *Wagneriana*: taxonomic history and remaining questions

The genus *Wagneriana* was erected by F.O. Pickard-Cambridge in 1904 in order to substitute the preoccupied name *Wagneria*. The latter name had been proposed by H. McCook in 1898 to allocate the species *Epeira tauricornis* O. Pickard-Cambridge, 1889. Pickard-Cambridge (1904) also proposed an identification key, illustrations and descriptions for all the *Wagneriana* species known until 1904: *W. tauricornis* (O. Pickard-Cambridge, 1889), designated as the type species, *W. spicata* (O. Pickard-Cambridge, 1889), *W. undecimtuberculata* (Keyserling, 1865) and *W. carinata* F. O. Pickard-Cambridge (1904). It

should be noted that in the original description of *W. tauricornis*, O. Pickard-Cambridge (1889) commented that this species “is one of a group which marks the transition to the Gasteracanthidae” and mentioned that “it might well form the type of a genus separate from *Epeira*”. Moreover, O. Pickard-Cambridge’s (1889) *Wagneriana* descriptions highlighted the presence of “grey hairs” in the cephalothorax and emphasized the strong variation in the size of abdominal tubercles and abdominal coloration within *W. tauricornis*, and the presence of strong spines in the thoracic groove of *W. spicata* as characteristic features of these species.

After these pioneering works, between 1935 and 1953 three additional species of *Wagneriana* were described: *W. grandicornis* Mello-Leitão, 1935 from Pernambuco, Brazil, *W. vermiculata* Mello-Leitão, 1949 from Mato Grosso, Brazil and *W. turrigera* Schenkel, 1953 from Venezuela. *W. grandicornis* and *W. vermiculata* were described based on juvenile specimens and *W. turrigera* based on a female specimen. Then, in 1954, Caporiacco transferred the species *Acrosoma transitorium* Koch, 1839 and *Epeira jelskii* Taczanowski, 1873 to *Wagneriana*. These species were described before the type species of the genus but were overlooked by Pickard-Cambridge (1904).

In 1991, as a part of his Araneidae monographies, H.W. Levi conducted the taxonomic revision of *Wagneriana*. In this work, an updated description and diagnosis for the genus was proposed, 25 new species were described, seven new combinations of species previously described in the genera *Actinosoma* Holmberg, 1883, *Edricus* Cambridge, 1890, *Wixia* Cambridge, 1882 and *Paraverrucosa* Mello-Leitão, 1939 were established, two synonyms at the generic level were suggested, and updated distribution maps and an identification key for all *Wagneriana* species were presented.

Levi (1991) did not test the monophyly of *Wagneriana* neither its phylogenetic placement, but he suggested as synapomorphies the glabrous often dark sides of the carapace, the presence of macrosetae in the thoracic groove, the shape of the paramedian apophysis, the modifications in the base of the median apophysis and the position of the tubercles in the abdomen.

Levi’s (1991) description of the genus *Wagneriana* stressed similarities with several Araneinae genera: position of abdominal tubercles (as in *Edricus* and *Parawixia* F. O. Pickard-Cambridge, 1904), epigynum shape (*Edricus*), presence of macrosetae in the fourth trochanter (*Parawixia* and *Wixia*) and terminal apophysis shape (*Edricus* and *Parawixia*). Levi (1991), also highlighted some of the remaining issues after his revision. First, he asserted that the placement of *W. turrigera* in the genus had been made “for convenience” and that “it may have to be placed in a new genus when males are found”. Second, he mentioned that “The separation

and determination of specimens of *W. heteracantha*, *W. neglecta*, and *W. eupalaestris* remains uncertain, as is the separation of the females of *W. transitoria*, *W. jelskii*, *W. maseta*, and *hassleri* and *silvae*". In relation with the latter aspect, he also stressed that "In all species there is considerable individual variation in markings and in color, size, length, and prominence of tubercles, and the length of the postanal tail", and he also mentioned that "Most species are surprisingly similar in appearance and cannot be separated by color pattern or body shape; they have to be separated by the genitalia". Finally, Levi (1991) asserted that the match between male and female was uncertain for the species *W. jelskii* (Taczanowski, 1873), *W. taim* Levi, 1991 and *W. atuna* Levi, 1991. In addition, Levi (1991) described nine species based only on one sex, three from males and six from females, leaving the description of the remaining sexes as future tasks.

After Levi's (1991) revisionary work, three additional species were described: *W. levii* Pinto-da-Rocha & Buckup, 1995 from Brazil, *W. fina* Alayón, 2011 from Cuba and *W. vallenuevo* Alayón, 2011 from Dominican Republic. Furthermore, the males of *W. roraima* Levi, 1991 and *W. yacuma* Levi, 1991 were described (Buckup & Pinto-Da-Rocha, 1996). Currently, *Wagneriana* includes 43 species distributed from southern United States to Argentina.

Despite the relatively well-established alpha taxonomy, the phylogeny of *Wagneriana* remains poorly studied since only two phylogenetic analysis have included a *Wagneriana* species in the taxon sampling. Magalhães & Santos (2012) included *W. dimastophora* (Mello-Leitão, 1940) as an outgroup for their *Micrathena* species-level phylogeny. In their analysis, *W. dimastophora* was recovered as the sister group of *Actinosoma pentacanthum* (Walckenaer, 1841). However, due to the few Araneidae genera included in this study, relationships among outgroups should be assessed with caution (Magalhães & Santos, 2012). For example, the unambiguous synapomorphies optimized for the clade *Wagneriana* + *Actinosoma* (*i.e.* presence of conductor gutter and base of median apophysis extended beneath radix), are also present in other genera not included in the analysis such as *Alpaida* O. Pickard-Cambridge, 1889 and *Edricus*. Conversely, in the ongoing study of the phylogeny of Araneidae (see section 1.3), the species *W. tauricornis* (O. Pickard-Cambridge, 1889) was recovered as part of the well-supported clade (*Parawixia* (*Alpaida Wagneriana*)) (D. Dimitrov pers. com.). Nevertheless, putative related genera of *Wagneriana* as *Edricus*, *Rubrepeira* Levi, 1992, *Actinosoma* and *Witica* O. Pickard-Cambridge, 1895 were not considered in the analysis. As such, the phylogenetic placement of *Wagneriana* as well as its species-level phylogeny, never assessed before, remain open questions. Considering the *status quo* of spiders systematics (see

section 1.1), these questions should be assessed with the greatest quantity of evidence combining phenotypic and genotypic characters.

The feasibility to collect *Wagneriana* in the field (see abundance of some species in several spider surveys: Pérez-de-la Cruz *et al.*, 2007 in Mexico, Bonaldo & Dias, 2010; Nogueira *et al.*, 2006; Podgaiski *et al.*, 2007 and Ricetti & Bonaldo, 2008 in Brazil, Deza & Andía, 2009 in Peru and Ferreira-Ojeda *et al.*, 2009; Pinzon *et al.* 2010 and Escorcía *et al.*, 2012 in Colombia) guarantees the possibility of obtaining fresh material and genotypic evidence with the traditional Sanger sequencing. In addition, as highlighted by Levi's (1991) revision, genital morphology and some somatic characters exhibit great variation across *Wagneriana* species, which can be turned into evidence to test phylogenetic hypotheses. Consequently, besides contributing to elucidate the phylogenetic relationships of a portion of one of the most problematic Araneidae lineages (*i.e.* the so-called Araneinae subfamily), testing *Wagneriana* monophyly and inferring its species-level phylogeny can also be a great opportunity to assess the impact of phenotypic characters in a molecular-dominated matrix. Moreover, in the light of new evidence, the remaining alpha taxonomy issues of the genus (*e.g.* sex matching, species identity) may be solved.

It should be considered that any research in systematics, including in this particular case the study of *Wagneriana* phylogeny, is developed in the context of exciting discussions. Currently, several ontological and epistemological debates remain open within systematics and consensus appear difficult to reach in several cases. These debates can be: 1) unknown due to the vast available literature or due to a biased reading, 2) known but regarded as irrelevant by the researcher or 3) known and considered highly relevant. In the following section, I present a synthesis of some of the most intensely debated topics in systematics that, in my opinion, should be faced in any study. Taking a side in some of these discussions is not a trivial choice since strong empirical effects can emerge after this decision.

1.5 Systematics: open debates

In order to facilitate the synthesis of some open debates within systematics, a schematic flowchart of the phylogenetic analysis process, considering ideas from different schools of thought (Holder & Lewis, 2003; Wheeler *et al.*, 2006; Yang & Rannala 2012; Nascimento *et al.*, 2017), is shown in Figure 1. In each portion of this diagram, I highlight some of the ontological, epistemological and empirical questions that may be addressed and point out some

of the aspects that have been the subject of intense debates¹.

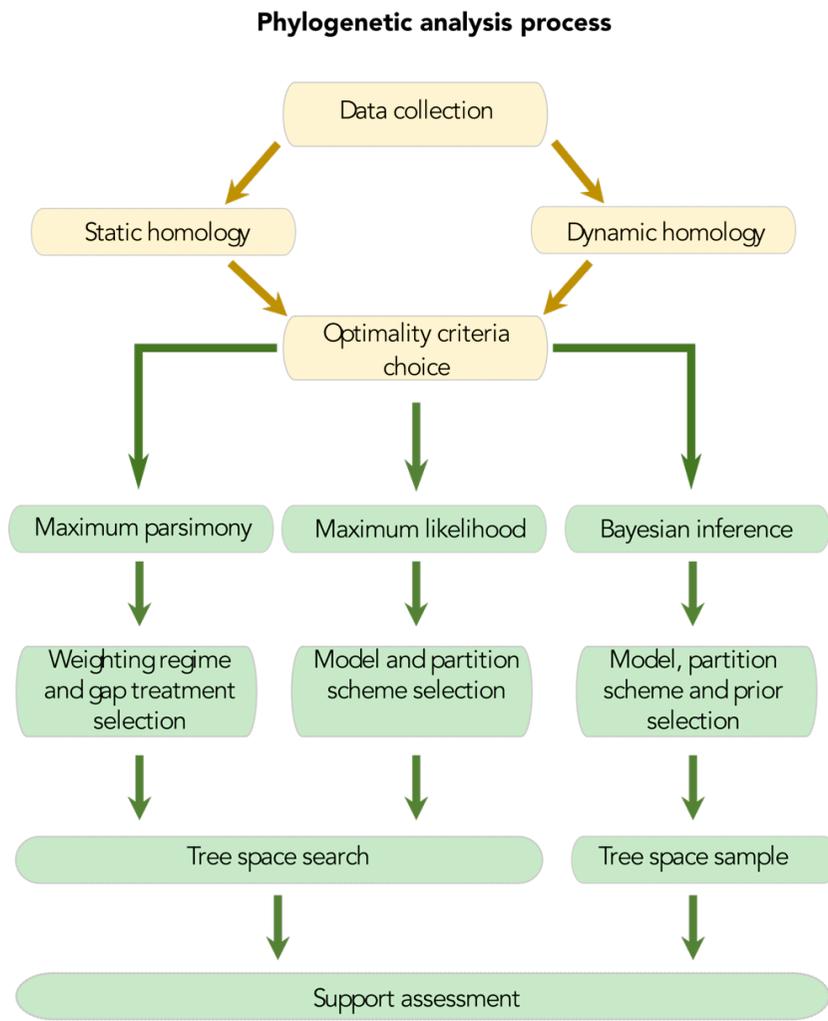
1.5.1. Character

Although characters are considered the basis of systematic analysis (Wheeler, 2012), their ontological status remains controversial (Colless, 1985; Wagner 2001; Richards, 2003; Grant & Kluge, 2004; Sereno, 2007; Rieppel, 2006; Rieppel & Kearney, 2007; Göpel & Richter, 2017). According to Grant & Kluge (2004), the most significant level of confusion when assessing the ontological status of character is between similarity-based and event-based character concepts. Grant & Kluge's (2004) distinction is highly relevant since it is directly related with the classes/individuals dichotomy, which has been involved in debates such as the concept of species (Zachos, 2016) and homology (see section 1.5.2).

In order to understand why Grant & Kluge's (2004) distinction is relevant for discussing the ontological status of character, it is crucial to identify the differences between classes and individuals. Classes are abstract and consequently cannot engage in processes. In addition, they are spatio-temporally unrestricted, have defining properties and instances. Conversely, individuals are concrete and can engage in processes such as evolution. Moreover, they are spatio-temporally restricted, have no defining properties and fulfill the principle of noninstantiability (Ghiselin, 1997, 2005).

Considering Ghiselin's (1997, 2005) characterization of classes and individuals, class-based concepts would be questionable within evolutionary biology because classes, by definition, are not able to evolve. Therefore, character concepts which use *definiens* such as properties, attributes, features and similarity would face an ontological discrepancy (see some examples in Sereno, 2007). On the contrary, character concepts focused on historical transformations do not face this contradiction. Hennig's (1966) concept is a significant contraposition to class-based concepts, since character is defined as a transformation series. Grant & Kluge (2004, see also Kluge & Grant, 2006) further delineated Hennig's (1966) concept as an event-based concept in which the hypothetical transformation series includes a transformation event(s) and a transformed object(s). The transformation event(s), which is never observed directly, is causally related to phylogeny and the transformed object(s) (*i.e.* the

¹My selection of debates does not aim to be exhaustive as the literature is rather vast. Nevertheless, I consider that my choice gathers together some of the most influential discussions that, in one way or another, may be related with controversies that I did not explicitly mention.



Ontological/Epistemological questions	Empirical questions
What is evidence?	How to establish morphological hypotheses of homology?★
What is species?	
What is character?★	Which alignment algorithm should be used?★
What is homology?★	
Which is the epistemological justification for using an optimality criterion?★	Which optimality criterion should be used?★
Which inference mode should be used: deductive, inductive or abductive?★	Which weighting regime should be used?★
What is probability?	Which gap treatment should be used?★
What is model?	Which criterion for model selection should be used?
What is stochasticity?	Which set of models should be assessed?★
What is support?★	Which search strategy should be used?
	Which prior should be used for each parameter?
	Which sampling strategy should be used?
	Which convergence diagnostic should be used?
	How to summarize the posterior distribution of trees and parameters?
	Which support measure should be used?★

Figure 1. Phylogenetic analysis process. Blue stars denote debate topics that are synthesized in the section 1.5.

least inclusive historical individual that result from heritable transformation events), is expressive of certain of the knowable characteristics of the event that can be exemplified in sense-experience (Grant & Kluge, 2004; Kluge & Grant, 2006).

Some researchers have focused their criticism against the event-based character concept in the lack of an explicit empirical operation for character definition and delimitation (*e.g.* Sereno, 2007; Assis & Brigandt, 2009). Within class-based concepts, the principal tool employed to delineate characters is similarity (Rieppel & Kearney, 2002). Nevertheless, proponents of the event-based character concept have also recognized the operational value of similarity, but they have clearly defined the conditions in which similarity would be useful. Kluge & Grant (2006, p.279), succinctly stated that “The bottom line is that the concept of similarity is irrelevant to the evolutionary scientist. Similarity may be useful operationally, but only insofar as it facilitates the ostensive (by reference, pointing, or enumeration) or extensional (denotative) definition of character-states in the delimitation of what are hypothesized transformation series, of which the transformation event(s) are a part”.

It should be noted that Grant & Kluge (2004) also stressed the importance of establishing an internally consistent character concept in order to develop valid discovery operations (see Grant, 2002) and to identify relevant data within phylogenetic inference. Grant & Kluge (2004) asserted that their concept renders non-heritable variation (*e.g.* variation due to environmental factors) and changes in frequency of states in populations as evidentially irrelevant, which clearly denote empirical implications for phylogenetic studies.

Currently, it is not a common practice that systematists explicitly state their character concept in papers (but see Grant *et al.*, 2006; Álvarez-Padilla & Hormiga 2011). Nevertheless, employing a class-based or an event-based character concept may generate some empirical discrepancies. These differences are more evident when systematists deal with highly similar or identical objects as arthropods setae and nucleotides, respectively (Kluge & Grant, 2006; Agolin & D’Haese, 2009).

1.5.2. Homology

Although ideas and discussions about the ontological status of homology are as old as the biological knowledge itself (Russell, 1916), the homology concept is currently one of the most hotly debated topics within systematics. Wheeler (2012) presented a synthetic review of some of the main conceptual shifts along the history of the homology concept, revealing an interesting path that to some extent echoes the history of systematic schools.

Between 2012 and 2014, 68 pages within the journal *Cladistics* were dedicated to discuss the ontological status of homology (Brower & de Pinna, 2012, 2014; Farris, 2012a, b, 2014a, b; Nixon & Carpenter, 2012a, b, c, 2013; Williams & Ebach, 2012; Assis 2013; Platnick, 2013). In these papers two main theses were discussed. Nixon & Carpenter (2012) defined homology as similarity due to common ancestry and considered synapomorphy and symplesiomorphy as types of homology. Conversely, Brower & de Pinna (2012) maintained the view that homology is a synonym of synapomorphy, a position that was previously defended by Patterson (1982) and de Pinna (1991).

According to Nixon & Carpenter (2012a, p.162) “If homology is similarity due to the occurrence of the same condition in the most recent common ancestor, then symplesiomorphic features satisfy this requirement just as do synapomorphic features” Contrariwise, Brower & de Pinna (2014, p.333) considered that “... symplesiomorphies only “exist” by complementary exclusion in a scheme of synapomorphies, and to reify them as entities with evidentiary status equivalent to synapomorphies undermines the basic premise of the Hennigian enterprise—that homologues inform us about relationship”. The debate is still open and no consensus appears visible in the near future.

It should be stressed that the classes/individuals dichotomy and its effects into the ontological discussions of biology, a central topic in the character concept debate (see section 1.5.1), were not directly considered in any of the *Cladistics*' papers mentioned previously. Nevertheless, as a consequence of the distinction between classes and individuals, Grant & Kluge (2004) proposed a different homology concept that offers an alternative ontological position to be consider. According to Grant & Kluge (2004) “Homology refers to the relation between parts that resulted from the same heritable transformation event. As such, homology = historical identity, i.e. two or more parts that are homologous are parts of the same historical individual”. In addition, for Grant & Kluge (2004) “synapomorphy refers to the shared occurrence of a derived (apomorphic) character-state, whether or not that shared occurrence resulted from the same transformation event (homology) or different transformation events”. Grant & Kluge's (2004) homology concept was also supported by Wheeler *et al.* (2006, see also Wheeler, 2012) who proposed that “Features are homologous when their origins can be traced to a unique transformation on the branch of a cladogram leading to their most recent common ancestor”. Remarkably, excluding similarity as a *definiens* of homology, as Grant & Kluge (2004) and Wheeler *et al.* (2006) proposed, establishes a concept of homology coherent with an alternative empirical avenue within phylogenetic studies in which the establishment of

hypothesis of homology and the congruence test are joined in a unique step. This approach can be traced back to Sankoff (1975), Sankoff & Cedergren (1983) and Wheeler (1996).

In a traditional static homology analysis, there are two basic steps: hypothesis generation (primary homology *sensu de Pinna, 1991*) and hypothesis legitimization (secondary homology *sensu de Pinna, 1991*). Remane's (1952) principles of similarity are widely used to establish primary homology for morphological characters and similarity algorithms are employed to establish primary homology among molecular characters (Wheeler, 2012). Each column in the resulting morphological matrix or multiple sequence alignment, represent a hypothesis of homology that is never submitted to additional test (De Laet, 2005, p. 94; Brower & de Pinna, 2012, p. 534) After this initial stage, a second step, the congruence test, is conducted and hypothesis of homology within states are corroborated or falsified. Conversely, within the dynamic homology approach, the dichotomy primary and secondary homology is dissolved (Grant & Kluge 2004) and the problem of aligning nucleotides into homologous characters is considered as inseparable from the problem of phylogenetic inference (Padiál *et al.*, 2014). As such, there are not *a priori* defined hypothesis of homology and characters are created and destroyed generating topology-specific homology regimes (Wheeler, 2001, 2002; Ramírez, 2007).

Within the parsimony context, using the static or the dynamic approach of homology is not a trivial topic, as topological changes have been obtained in simulated and real data-sets when one of these approaches is preferred (Ford & Wheeler, 2016). Within the context of maximum likelihood and Bayesian inference the static homology approach is the widespread position, and as such, the similarity-based concept of homology is assumed. Nevertheless, in these optimality criteria any consistent ontological statement should explicitly include a probabilistic assertion (see Assis, 2015 for the case of synapomorphies).

It is interesting to note that the establishment of homology hypotheses is one of the most fundamental, sometimes overlooked, aspect in the bioinformatics pipelines for processing and analyzing NGS data (Springer & Gatesy, 2018). In addition, though out of the scope of this synthesis, homology assessment methods in phylogenomic datasets have benefited when clear ontological status for terms like orthology and paralogy has been defined (Gabaldón, 2008; Gabaldón & Koonin, 2013; Ballesteros & Hormiga, 2016).

1.5.3. Optimality criteria and inference modes

In any phylogenetic analysis, the number of possible phylogenetic hypotheses is merely a function of the number of terminals. As such, systematists have to use an objective function to assess the relative quality of these hypothesis (Wheeler, 2012). As Wheeler (2012, p. 49) succinctly stated “trees must have a cost ... Without such a cost, these objects are mere pictures ... of no use to science”. Nevertheless, there is no agreement about which optimality criterion should be used to assess the quality of phylogenetic trees (but see Whelan & Morrison, 2017; Puttick *et al.*, 2017). Usually, distance, parsimony, maximum likelihood and Bayesian inference are considered the main types of optimality criteria for hypothesis choice (Swofford *et al.*, 1996; Felsenstein, 2004; Yang, 2006, 2014; Lemey *et al.*, 2009; Wheeler, 2012; Yang & Rannala, 2012; Whelan & Morrison, 2017). Strengths and weaknesses of each method from the philosophical and the statistical points of view have been the basis for vast discussions to justify the preference for one criterion over another and a consensus seems difficult to reach (see for example Felsenstein, 1978; Farris, 1983; Huelsenbeck, 1995; Chang, 1996; Kluge, 1997a; Siddal & Kluge, 1997; Farris, 1999; Sanderson & Kim, 2000; Swofford *et al.*, 2001; Goloboff, 2003; Goloboff & Pol 2005; Kolaczkowski & Thornton, 2004, 2009; Huelsenbeck *et al.*, 2011; Yang & Rannala, 2012; Padial *et al.*, 2014; Editors, 2016; Gillerme & Cooper, 2016; Brower, *In Press*; Goloboff *et al.*, *In press*). Although in several cases using different optimality criteria with the same dataset may result in topologies with minor differences (Rindal & Brower, 2011) this is not always the case (Padial *et al.*, 2014; Goicoechea *et al.*, 2016), therefore optimality criteria choice is a crucial step in any phylogenetic analyses.

Nowadays it seems to be a common practice to make a somewhat eclectic choice among optimality criteria. Clades recovered by several criteria are considered as more supported than clades obtained by just one (*e.g.* Parry *et al.*, 2017). However, this sort of analysis (*i.e.* methodological concordance) has been criticized as no explicit justification is usually offered for this position (Grant & Kluge, 2003). A related issue that has been discussed is the validity of sensitivity analyses *sensu* Wheeler (1995, see also Giribet, 2003) as a test for phylogenetic hypotheses (Grant & Kluge, 2005; Giribet & Wheeler, 2007).

It should be noticed that one aspect rarely acknowledged by systematists when choosing among optimality criteria is that this choice also implies adopting a particular inference mode. Within science, three types of inference are traditionally recognized: deduction, induction and abduction (Fitzhugh, 2006; Wheeler, 2012; Woo *et al.*, 2016). Deduction is the process of reaching a logical conclusion based on premises, if the premises are true the result must be true. Induction is a process of generalizing results beyond the observations at hand. Finally, abduction implies deriving the best or most feasible explanation for a phenomenon (for a

detailed presentation of abductive reasoning within phylogenetic inference see Fitzhugh, 2006). Wheeler (2012) also recognized a variant of the deductive mode of inference, the so-called hypothetico-deductive model, which explicitly uses falsification through the *modus tollens*.

According to Woo *et al.* (2016) a good balance of deduction, induction and abduction are symptoms of a healthy science, since the three types of inference may be involved in generating and testing hypotheses. In the particular case of phylogenetic analyses, Wheeler (2012, p. 74) proposed an inferential scheme in which the hypothetico-deductive model is depicted as a combination of the three modes of inference. Furthermore, Wheeler (2012) characterized the optimality criteria traditionally used according with these inferential modes. In parsimony, the hypothetico-deductive model is explicitly used as the least falsified hypothesis is most favored. In maximum likelihood, the hypothesis that maximizes the probability of the data is considered the best explanation, characterizing a typical abductive inference, and lastly, in Bayesian inference, the calculation of clade posterior probabilities is conducted from a limited sample of trees, which exemplifies a standard inductive process (Wheeler, 2012).

Finally, it is interesting to note that even within an optimality criterion some topics have been the subject of debate. For example, within parsimony three different epistemological justifications have been proposed: minimization of *ad hoc* hypotheses of homoplasy (Farris, 1983), minimization of *ad hoc* hypotheses of transformation events (Kluge & Grant, 2006; Grant & Kluge, 2009) and maximization of the amount of similarity that can be interpreted as homology (De Laet, 2005; 2015). Recently, Ospina-Sarria & Cabra-García (*In press*) have suggested some clarifications and advice to be consider when discussing the epistemological justification of parsimony in phylogenetic inference.

1.5.4. Weighting

Within parsimony, Kluge (1997b) and Goloboff *et al.* (2008b) are among the most noticeable authors against and in favor of differential weighting of evidence in phylogenetic analyses, respectively. Kluge (1997b), considering the interplay between evidence (e), hypotheses (h) and background knowledge (b) within Popper's degree of corroboration (C) and severity of test (S) formulas, asserted that any weighting scheme negatively impacts C and S, either by adding to b, or by reducing the empirical content of h. In addition, Kluge (1997b) presented some cases in which implied weighting (see Goloboff, 1993) considered least parsimonious trees as optimal. According to Kluge (1997b), these hypotheses should be

considered more *ad hoc*, and as such, worse explanations. Finally, Kluge (1997b) criticized the use of hypothesized homoplasy quantity as a criterion to down-weight characters, since independently evolved states by definition are historically unique and, therefore, there is no basis to count hypothesized instances of homoplasy as if they were the same.

Goloboff *et al.* (2008b) criticized the philosophical arguments of Kluge (1997b) mentioning that Popper's formulas were never meant to apply in real cases and that Kluge did not show how weighting decreases C or S. In addition, Goloboff *et al.* (2008b) considered that parsimony, according to Farris (1983), is not equivalent to equal weights, and that steps counts must be weighted step counts. Finally, Goloboff *et al.* (2008b) stressed that Kluge (1997b) did not offer any empirical evidence to support his assertions. On the contrary, Goloboff *et al.* (2008b) conducted a series of empirical analyses with different datasets demonstrating that: 1) jackknife frequencies in large molecular data sets are actually improved when downweighting characters according to their homoplasy, 2) downweighting characters according to their homoplasy in morphological data sets increases jackknife frequencies, and 3) results obtained under homoplasy weighting are more stable to adding either taxa or characters in relation to equal weights.

The methodological positions of Kluge (1997b) and Goloboff *et al.* (2008b, see also Goloboff, 2015) have been followed by several authors, and, as numerous topics summarized in this section, a consensus seems difficult to be reached in the near future. It is worth noting that some of the arguments against weighting are similar to those used to criticize the use of models in phylogenetic inference (see section 1.5.6).

1.5.5. Insertion and deletion events

Insertion and deletion events (indels) are transformational events that molecular sequences may exhibit along evolution. Therefore, as any heritable transformation (*e.g.* transitions and transversions), indels can be used as evidence to test phylogenetic hypotheses (Wheeler, 1996; Giribet & Wheeler, 1999; Simmons & Ochoterena, 2000; Denton & Wheeler, 2012). Indel events are represented by gaps in multiple sequence alignments and its quantity and distribution are greatly influenced by the alignment algorithm and the cost matrices used. These properties can have strong topological impacts in the optimal tree (Ford & Wheeler, 2016).

Yang (2014) mentioned three *ad hoc* procedures for treating gaps in a given alignment: 1) treating the gap as the fifth nucleotide or the 21st amino acid, with the concomitantly problem of considering a stretch of continuous gaps (*e.g.* five gaps) as independent

evolutionary events, even though it may represent one event, 2) delete all sites at which there are alignment gaps and 3) treat alignment gaps as undetermined nucleotides. Yang (2014) explicitly considered options two and three as the worse possibilities but at the same time the most commonly used. Adopting option two can lead to an unjustified deletion of evidence and implementing option three may be a possibly unique case in which evidence of absence is treated as absence of evidence (Padial *et al.*, 2014).

Optimality criteria choice (see section 1.5.3) may also be influenced by gap treatment. Parsimony approaches, either static or dynamic, treat gaps as a fifth character state. Conversely, because of computational constraints, the most commonly used programs for maximum likelihood and Bayesian inference treat gaps as nucleotides of unknown identity (see manuals of RAxML, MrBayes, IQtree, Garli and Beast).

1.5.6. Nucleotide substitution models

The number of mutation events that occurred in a certain time period can be modelled as a Poisson process. This process can be generalized to a Markov process which uses a Q matrix that specifies the relative rates of change of each nucleotide. In all Markov processes the conditional probability of change at a site in a sequence depends only on the current state and is independent of previous states, according to Yang (2014, p. 1) “given the present, the future does not depend on the past”. In addition to this Markovian property, Markov models of nucleotide substitution assume that the evolutionary process at each site is stationary, reversible, and homogeneous (Bryant *et al.*, 2005; Strimmer & von Haeseler, 2009; Jermini *et al.*, 2017). Stationarity implies that the marginal probability of the nucleotides remains the same (*i.e.* the relative frequencies of each nucleotide are the same), reversibility implies that the probability of sampling nucleotide *i* from the stationary distribution and going to nucleotide *j* is the same as the probability of sampling nucleotide *j* from the stationary distribution and going to nucleotide *i*, and homogeneity implies constant rates of change over an edge (*i.e.* substitution rates do not change over time) (Strimmer & von Haeseler, 2009; Jermini *et al.*, 2017).

As Strimmer & von Haeseler (2009) asserted, assumptions of Markov models are not necessarily biologically plausible, they are the consequence of modelling substitutions as a stochastic process. This aspect is precisely one of the main arguments that has been used to criticize how Markov models are being used in phylogenetic inference. Jermini *et al.*, (2017) and Padial *et al.* (2014) exemplify two opposing views about the lack of biological realism in Markov models.

Jermiin *et al.*, (2017) stressed that a growing body of data suggest that sequences have evolved under more complex conditions as those implied by stationarity, reversibility, and homogeneity. As such, they considered unwise to use popular implementations of model-selection methods that restrict the users to Markov models that satisfy these properties. It is worth noting that models implemented in commonly used programs such as RAxML (Stamatakis, 2014), Garli (Zwickl, 2006) and MrBayes (Ronquist *et al.*, 2012), assume stationarity, reversibility, and homogeneity; IQtree (Nguyen *et al.*, 2015; Kalyaanamoorthy *et al.*, 2017) and PhyloBayes (Lartillot *et al.*, 2009) being noticeable exceptions. Jermiin *et al.*, (2017) suggested to conduct tests for detecting heterogeneity across sequences as well as exploring nonreversible Markov models as standard practices in phylogenetic analyses.

Conversely, Padial *et al.* (2014) criticized the use of Markov models of nucleotide substitutions, relating them with methods that differentially weight characters according to their intrinsic reliability. According to Padial *et al.* (2014) models currently used are just speculations based on what people believe to be more-or-less plausible and have been defined more by the simplicity of mathematical calculations and avoidance of statistical inconsistency than by biological realism. The lack of biological realism is further emphasized by Padial *et al.* (2014), criticizing the treatment of gaps as undetermined nucleotides in commonly used phylogenetic programs (see section 1.5.5). Finally, Padial *et al.* (2014) stressed that systematists abandon scientific realism in favor of instrumentalism when embracing the use of models, replacing scientific theories as candidates for truth or reference by hypotheses that are more or less useful.

1.5.7. Support

When discussing support measures in systematics, Wheeler (2012) asserted that “There can be no single “best” support value given that the goals of different investigators and support indices vary”. This affirmation concisely describes the current situation in relation with support measures within systematics. There are two main groups of support measures that strongly differ in their theoretical basis and empirical interpretations: resampling measures and optimality-based measures (Wheeler, 2012). Resampling measures (*e.g.* jackknife, bootstrap, symmetric resampling) quantify support as the relative amount of favorable and contradictory evidence for each group present in the optimal topology (Goloboff *et al.*, 2003; Ramírez, 2005, but see Yang, 2014 for alternative interpretations). Conversely, optimality-based measures quantify support comparing the cost (length, parsimony score, likelihood, posterior probability) of the best tree in relation with suboptimal trees (Wheeler, 2012).

Grant & Kluge (2008a) established two adequacy conditions that must be met in order for a method to provide a measure of objective support. First, support and optimality must vary in direct proportion to each other. This condition prevents paradoxical cases in which suboptimal hypotheses are considered to have greater support than optimal hypotheses. Second, the measure must quantify support in terms of explanatory power. According to Grant & Kluge (2008a), the Goodman-Bremer support (Grant & Kluge, 2008b) and the ratio of explanatory power (Grant & Kluge, 2007) satisfy both conditions, and as such, must be considered objective measures of support. Conversely, measures that only satisfy the first adequacy condition (*e.g.* likelihood ratio, likelihood difference, posterior probability ratio and posterior probability difference) or do not satisfy neither of these (*e.g.* relative fit difference, resampling techniques and Markov Chain Monte Carlo clade frequencies) should not be considered as objective measures of support. Wheeler (2012) did not explicitly mention Grant & Kluge's (2008a) position, however he asserted that one of the advantages of the optimality-based support measures is that its meaning is clear: "The support value for a given vertex is a function of the best (optimal) tree with that node, and the best tree without".

Support measures are generally used to judge the quality of a certain phylogenetic hypothesis and the informativeness of the data at hand. Nevertheless, as presented in this section, the interpretation of a certain support measure should be made cautiously in the face of the contrasting meanings of support in phylogenetic inference.

CONCLUSIONS

- Even accounting for 2.80-3.05% of the total evidence matrices (167 morphological characters vs. 5303 aligned nucleotides in similarity alignment and 5946 in tree alignment), the employed phenotypic characters had impacts in the support values and phylogenetic significance (*i.e.* topological effect). In general, the inclusion of phenotypic evidence, irrespective of the optimality criterion used, increased the support values of several ingroup and outgroup clades. Furthermore, the monophyly of some clades (*e.g.* *Parawixia*, *Paraverrucosa*) was only recovered with the addition of phenotypic characters. These results stress the importance of considering phenotypic evidence in phylogenetic analyses, even in cases with a high disproportionality between genotypic and phenotypic evidence.

- The topological comparisons conducted across diverse analytical approaches suggest that optimality criterion and alignment method have phylogenetic significance. Remarkably, the election of alignment criteria (similarity alignment vs. tree alignment) has comparable

topological effects to that of optimality criteria choice (parsimony, maximum likelihood or Bayesian inference).

- Phylogenetic analyses within the maximum likelihood context should explore the performance of multiple programs, since the program choice could affect the maximization of the likelihood score and the tree topology.

- In the face of topological differences, systematists should make a decision among the analytical criteria employed. The most widely used choice is to conduct multiple analytical criteria and to associate clade sensitivity to these criteria as a notion of support. An alternative position is to choose a particular approach and offer a rational justification for the election. The latter approach is followed here.

- As currently delimited, *Wagneriana* was not recovered as a monophyletic group. The species *W. carimagua* and *W. uropygialis* were nested within the genera *Parawixia* and *Alpaida*, respectively. In addition, the remaining *Wagneriana* species fell into three major clades, neither of which formed a pair of sister taxa: 1) the Clade I including *W. iguape* and *W. gavensis*, 2) the Clade II including *W. uzaga*, *W. neglecta*, *W. heteracantha* and *W. eupalaestra*, and 3) the clade *Wagneriana sensu stricto* including the type species *W. tauricornis*.

- The great majority of lineages within *Wagneriana* s.s. were delimited by homoplastic phenotypic synapomorphies; only two clades were delimited by unique and non-homoplastic ones.

- Considering the phylogenetic results, a new genus is proposed (*Popperaneus*) and the genus *Paraverrucosa* is resurrected. Both genera allocate *Wagneriana* species that were recovered outside the *Wagneriana* s.s. clade.

- Six new combinations are proposed: *Popperaneus gavensis* (Camargo, 1950), *Popperaneus iguape* (Levi, 1991), *Paraverrucosa uzaga* (Levi, 1991), *Paraverrucosa heteracantha* (Mello-Leitão, 1943), *Parawixia carimagua* (Levi, 1991) and *Alpaida uropygialis* (Mello-Leitão, 1944).

- Two combinations are reestablished: *Paraverrucosa neglecta* Mello-Leitão, 1939 and *Paraverrucosa eupalaestra* (Mello-Leitão, 1943).

- Five species are newly described: *W.* sp. nov. 1 from the Peruvian and Ecuadorian Amazon regions, *W.* sp. nov. 2 known from Mexico to Ecuador, *W.* sp. nov. 3 from the Amazon regions of Brazil, French Guiana, Guyana and Peru, *W.* sp. nov. 4 known only from the type locality in the Brazilian Amazonas state and *W.* sp. nov. 5 from southern Brazil and northern Argentina.

- The following taxa are newly synonymized: *Marxia labidura* Mello-Leitão, 1943 with *Paraverrucosa eupalaestra* (Mello-Leitão, 1943), *Wagneriana levii* Pinto-da-Rocha & Buckup, 1995 with *Wagneriana taim* Levi, 1991, *Wagneriana fina* Alayón, 2011 with *Wagneriana atuna* Levi, 1991, *Wagneriana bamba* Levi, 1991 with *Wagneriana jelskii* (Taczanowski, 1873) and *Parawixia porvenir* Levi, 1992 with *Parawixia carimagua* (Levi, 1991)

- The following taxa are considered as *nomina dubia*: *Wagneriana vermiculata* Mello-Leitão, 1949 and *Wagneriana grandicornis* Mello-Leitão, 1935.

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