

UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**Cladistic analysis of Ophioninae Shuckard, 1840
(Hymenoptera, Ichneumonidae)**

ALESSANDRO RODRIGUES LIMA

Belo Horizonte, Minas Gerais

2019

Alessandro Rodrigues Lima

**Cladistic analysis of Ophioninae Shuckard, 1840
(Hymenoptera, Ichneumonidae)**

Tese apresentada à Coordenação do Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Instituto de Ciências Biológicas - UFMG, para a obtenção do título de Doutor.

Orientadora: Dra. Claudia Maria Jacobi

Co-orientadora: Dra. Alice Fumi Kumagai

Belo Horizonte, Minas Gerais

2019

043 Lima, Alessandro Rodrigues.
Cladistic analysis of Ophioninae Shuckard, 1840 (Hymenoptera,
Ichneumonidae) [manuscrito] / Alessandro Rodrigues Lima. - 2019.
111 f. : il. ; 29,5 cm.

Orientadora: Dra. Claudia Maria Jacobi. Co-orientadora: Dra. Alice Fumi
Kumagai.

Tese (doutorado) - Universidade Federal de Minas Gerais, Instituto de
Ciências Biológicas. Programa de Pós-Graduação em Zoologia.

1. Zoologia. 2. Vespas. I. Jacobi, Claudia Maria. II. Kumagai, Alice Fumi. III.
Universidade Federal de Minas Gerais. Instituto de Ciências Biológicas. IV.
Título.

CDU: 591

ATA DE DEFESA DE TESE DE DOUTORADO

Alessandro Rodrigues Lima

Ao vigésimo nono dia do mês de outubro do ano de dois mil e dezenove, às quatorze horas, na Universidade Federal de Minas Gerais, teve lugar a defesa de Doutorado da Pós-Graduação em Zoologia, de autoria do Doutorando Alessandro Rodrigues Lima intitulada: **"Cladistic analysis of Ophioninae Shuckard, 1840 (Hymenoptera, Ichneumonidae)"**. Abrindo a sessão, a Presidente da Comissão, Profa. Dra. Claudia Maria Jacobi, após dar a conhecer aos presentes o teor das Normas Regulamentares do Trabalho Final, passou a palavra para o candidato para apresentação de seu trabalho.

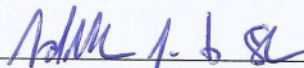
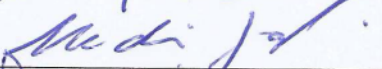
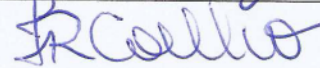
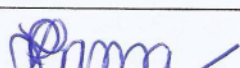
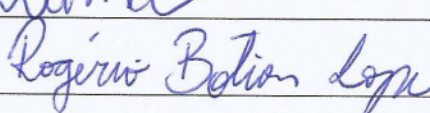
Esteve presente a Banca Examinadora composta pelos membros: Adalberto José dos Santos, Igor Rismo Coelho, Paula Caetano Zama, Rogério Botion Lopes, e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do candidato.

Após a arguição, apenas os Srs. Examinadores permaneceram na sala para avaliação e deliberação acerca do resultado final, a saber: o trabalho foi:

- Aprovado sem alterações
 Aprovado com alterações (observações em anexo)
 Reprovado

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 29 de outubro de 2019.

Comissão Examinadora	Assinatura
Prof. Dr. Adalberto José dos Santos	
Profa. Dra. Claudia Maria Jacobi (orientadora)	
Prof. Dr. Igor Rismo Coelho	
Profa. Dra. Paula Caetano Zama	
Prof. Dr. Rogério Botion Lopes	

ADVERTÊNCIA

De acordo com o Código Internacional de Nomenclatura Zoológica (CINZ), esta tese não é considerada uma publicação. Desta forma, as mudanças taxonômicas sugeridas aqui não têm nenhuma validade para a nomenclatura zoológica.

WARNING

According to the International Code of Zoological Nomenclature (ICZN), this thesis can not be considered as a publication. Therefore, the taxonomic changes suggested here are not valid in the zoological nomenclature.

“[...] There seems to me too much misery in the world. I cannot persuade myself that a beneficent & omnipotent God would have designedly created the **Ichneumonidae** with the express intention of their feeding within the living bodies of caterpillars[...].”

From Darwin's correspondence to Asa Gray, 1860

Acknowledgments

Aos representantes das instituições nacionais e internacionais citados na seção *Material and Methods* que enviaram material utilizado neste estudo; e aos que me receberam calorosamente em suas coleções, em especial Gavin Broad e Jaswinder Boparai (Londres); Michael Ohl (Berlin); e David Schimrosczyk (Varsóvia).

À minhas orientadoras Alice Fumi Kumagai e Claudia Maria Jacobi, que me deram muita liberdade para desenvolver a tese, e sempre estiveram disponíveis oferecendo suporte.

À minha família, em especial meus pais, Marta e Moacir, que fizeram muitos sacrifícios ao longo da vida para que eu pudesse estudar. Nada disso seria possível sem vocês.

À minha amada esposa, Michelle Villefort de Bessa Campos, companheira de vida e melhor amiga. Obrigado por tudo.

Aos amigos da UFMG (da biologia ou não) e Passo Básico Dança de Salão. Vocês facilitam muito a árdua tarefa de viver nesse Brasil (que eu amo).

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pelo apoio financeiro por meio da verba PROAP e pela manutenção do Programa de Pós Graduação em Zoologia da UFMG.

Summary

Resumo	1
Abstract	3
Introduction	5
Ichneumonidae	5
Ophioninae Shuckard, 1840	6
Phylogenies	9
Objectives	12
Material and methods	12
Terminology	12
Taxonomic sampling	16
Ingroup taxa	16
Outgroup taxa	18
Collections	18
Character circumscription	20
Phylogenetic analysis	21
Results and Discussion	22
Character list	22
Phylogenetic analysis	53
Remarks on selected characters	62
Taxonomy	72
Concluding Remarks	80
References	81
Appendix 1	85
Appendix 2	102
Annex I	110
Annex II	111

Resumo

Palavras-chave: Vespas de Darwin, vespas noturnas, parasitóides

Ophioninae é uma subfamília de Ichneumonidae diversificada e cosmopolita, com mais de 1.100 espécies descritas em 32 gêneros válidos. A maioria das espécies possui hábitos noturnos, com uma morfologia peculiar, denominada '*ophionoid facies*', o que inclui ocelos grandes, antenas longas e cor marrom-amarelada pálida. A primeira análise filogenética focada nos gêneros de Ophioninae foi realizada há 40 anos. Até agora, existem seis filogenias publicadas que lidam com o relacionamento dos gêneros, mas apenas duas dessas análises focaram toda a subfamília. Todas as filogenias usaram morfologia, isolada ou combinada com dados moleculares, mas diferenças nos métodos (critérios de otimização e software utilizado), amostragem de táxons (grupo interno e externo), uso de terminais específicos ou abstrações supra-específicas e definição dos caracteres e estados empregados. O objetivo aqui foi realizar uma análise cladística morfológica utilizando o critério de parcimônia, amostrando todos os gêneros de Ophioninae, utilizando espécies como terminais e definindo caracteres, e seus respectivos estados, de acordo com sua distribuição nos espécimes (contínuos x discretos). A codificação foi baseada na observação de 536 espécimes de 19 coleções em todo o mundo. A matriz construída foi analisada no TNT sob pesos iguais, utilizando os algoritmos da opção *New technology search* (Sec. search + Ratchet + Drift +Tree Fusing). Ao todo, 125 Ophioniformes foram utilizados como terminais, 114 Ophioninae e 11 espécies de outras subfamílias, usando *Stetanthyx lucasi* (Tersilochinae)

como referência para o enraizamento. Todos os 32 gêneros de Ophioninae foram incluídos, 24 deles representados pela espécie tipo. Os caracteres morfológicos utilizados nas filogenias anteriores (551 no total) foram reavaliados. Ao todo, 164 caracteres foram utilizados, incluindo alguns novos caracteres. A análise resultou em oito árvores igualmente parcimoniosas, corroborando a monofilia de Ophioninae, com Campopleginae como grupo irmão. Dentro da subfamília, o clado Hellwigiini **stat. rev.** incluindo *Heinrichiella*, *Hellwigia* e *Skiapus*, é grupo irmão dos Ophioninae restantes. A tribo Thyreodonini foi recuperada incluindo agora cinco gêneros, *Orientospilus*, *Euryophion*, *Dictyonotus*, *Rhynchophion* e *Thyreodon*. A tribo Ophionini foi recuperada como um clado, incluindo pela primeira vez *Prethophion*, *Stauropoctonus*, *Eremotylus* e *Trophophion*, além dos gêneros anteriormente considerados, *Sclerophion*, *Rhopalophion*, *Ophion*, *Alophophion*, *Agatophiona*, *Afrophion* e *Xylophion*. Não houve suporte para resolver a politomia entre as espécies de *Eremotylus* e o monotípico *Trophophion*. *Ophion*, como proposto atualmente não é monofilético com relação a quase todos os gêneros da tribo, exceto *Sclerophion* e *Rhopalophion*. A tribo Enicospilini está dividida em dois grandes clados. O primeiro inclui *Janzophion*, *Pamophion*, *Laticoleus*, *Lepiscelus*, *Simophion*, *Ophiogastrella* e *Leptophion*, todos, exceto *Laticoleus*, gêneros monofiléticos. O segundo clado inclui *Riekophion* (parte), *Dicamptus* e *Enicospilus* (que inclui *Sicophion* **syn. n.**). Duas novas tribos são propostas, Barytatocephalini **trib. n.** e Hellwigiellini **trib. n.**, incluindo respectivamente *Barytatocephalus* e *Hellwigiella*.

Abstract

Key-words: Darwin wasps, nocturnal wasps, parasitoids

Ophioninae is a large, worldwide subfamily of Ichneumonidae, with more than 1,100 species described in 32 valid genera. The majority of species have nocturnal habits, with a peculiar morphology, termed as the ‘ophionoid facies’, which includes large ocelli, long antennae, and pale yellow-brown color. The first phylogenetic analysis focusing on Ophioninae genera was performed 40 years ago. By now, there are six published phylogenies dealing with the generic relationship, but only two of them were targeting the whole subfamily. All phylogenies have used morphology, either alone or combined with molecular data, but they vary greatly in methods (optimization criteria and software), taxon sampling (ingroup and outgroup), use of specific or supraspecific terminals, and definition of the characters and states employed. The objective here was to perform a morphological cladistic analysis using the parsimony criterion, sampling all Ophioninae genera, using species as terminals, and defining characters and their states according to their distribution among specimens. The coding was based on the observation of 536 specimens from 19 collections around the world. The matrix built was analysed on TNT under equal weights, using New technology search algorithms (Sec. search + Ratchet + Drift +Tree Fusing). Altogether, 125 species were used as terminals, 114 Ophioninae and 11 Ophioniformes (outgroup), with *Stetanthyx lucasi* (Tersilochinae) as root. All 32 genera of Ophioninae were included, 24 of them represented by the type species. The morphological characters used in the previous phylogenies (551

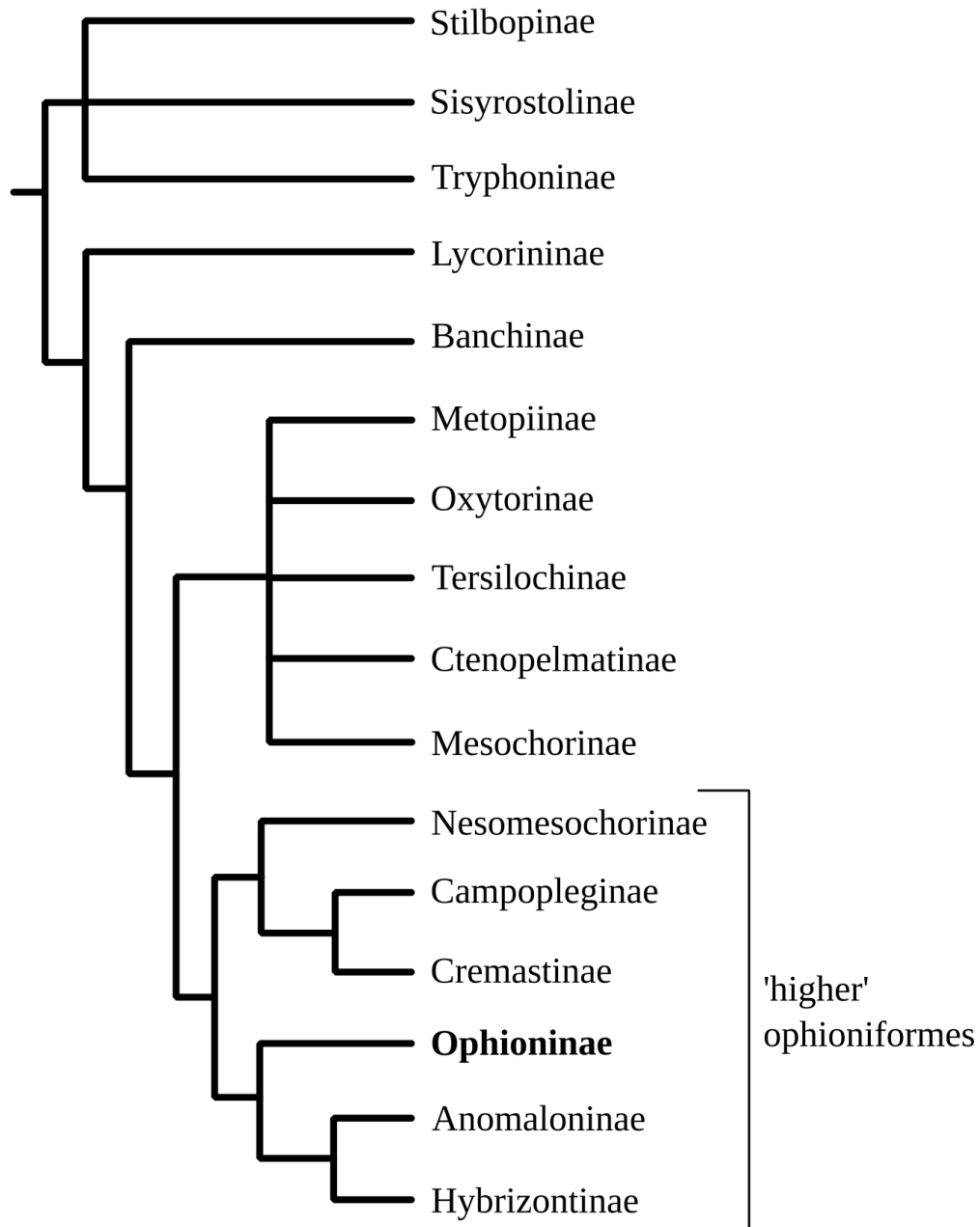
in total) were evaluated to be used. Altogether, 164 characters were employed, including some new propositions. The analysis resulted in eight equally parsimonious trees, which supported the monophyly of Ophioninae, with Campopleginae as the sister group. Inside the subfamily, the clade *Hellwigiini* **stat. rev.**, including *Heinrichiella*, *Hellwigia* and *Skiapus*, is sister group of the remaining Ophioninae. The *Thyreodonini* was recovered as a clade, including five genera, *Orientospilus*, *Euryophion*, *Dictyonotus*, *Rhynchophion* and *Thyreodon*. The *Ophionini* was recovered monophyletic, for first time including *Prethophion*, *Stauropocetus*, *Eremotylus* and *Trophophion*, besides the already included genera, *Sclerophion*, *Rhopalophion*, *Ophion*, *Alophophion*, *Agatophiona*, *Afrophion* and *Xylophion*. There is no support to define the polytomic relationship of *Eremotylus* species and the monotypic *Trophophion*. *Ophion*, as currently proposed is not monophyletic with respect to all genera in the tribe except *Sclerophion* and *Rhopalophion*, nonetheless, a single change is proposed, *Agathophiona* **syn. n.** The *Enicospilini* is divided into two clades. The first including *Janzophion*, *Pamophion*, *Laticoleus*, *Lepiscelus*, *Simophion*, *Ophiogastrella* and *Leptophion*, all monophyletic, except for *Laticoleus*. The second clade including *Riekophion* (part), *Dicamptus* and *Enicospilus* (including *Sicophion* **syn. n.**). Two new tribes are proposed, *Barytatocephalini* **trib. n.** and *Hellwigiellini* **trib. n.**, including *Barytatocephalus* and *Hellwigiella* respectively.

Introduction

Ichneumonidae

Ichneumonidae is one of largest Hymenoptera families, with more than 24,000 described species (Yu *et al.* 2012), and with an expectation of up to twice this amount in undescribed species (Gauld *et al.* 2002). Together with Braconidae, they form the superfamily Ichneumonoidea, all formed by parasitoid wasps, comprising species with almost all the known parasitoid strategies, such as idiobiosis, koinobiosis, ectoparasitoidism, endoparasitoidism, and even hyperparasitism. There is no definitive classification for Ichneumonidae, and the number of subfamilies vary from 35 to 48 according to different proposals, with some controversial groups sometimes considered as Braconidae or even distinct families. Here we adopt the classification summarized by Broad *et al.* (2018), which comprises 42 subfamilies.

The most comprehensive phylogenetic analysis of Ichneumonidae was by Quicke *et al.* (2009), who analysed a total evidence matrix with 1001 terminals. Leaving aside all possible criticisms to the unconventional methods used, this analysis represented a great step to understand the internal relations of the family. Quicke *et al.* (2009) found phylogenetic support for some groups of subfamilies that have long been proposed as informal groups, such as the Ophioniformes, first proposed by Gauld (1985). Inside the Ophioniformes, they recovered a clade named 'higher ophioniformes', including Anomaloninae, Campopleginae, Cremastinae, Hybrizontinae, Nesomesochorinae and Ophioninae (Fig.1).



OBJ

Figure 1. Strict consensus of the Ophioniformes, based on Qicke (2014) fig.13.1

Ophioninae Shuckard, 1840

Ophioninae is a large cosmopolitan subfamily, with about 1100 species described in 32 genera (Yu *et al.* 2012; Shaw & Voogd 2019). Adults are easily recognizable among Ichneumonidae on the basis of their morphology. Most species are nocturnal, having a pack of morphological adaptations to this

kind of life, termed the 'ophionoid facies' (Gauld & Huddleston 1976), including large ocelli, long antennae, and pale yellow-brown color (Fig.2A). Different from the Ichneumonidae forewing pattern, Ophioninae (except in *Skiapus*) have a single intercubital vein, which is distad of 2m-cu vein, and have a spurious vein in the forewing cell second subdiscal cell (=3Cu) subparallel to the posterior margin of the wing (Fig.2B–C) in most genera. Many other nocturnal Ichneumonidae genera exhibit the ophionoid facies, resembling Ophioninae, but they can be distinguished by the different wing venation. However, if on the one hand it is easy to identify an Ophioninae among the Ichneumonidae, due to its peculiar morphology, on the other hand the species or even genus-level identification is a complicated task due to their high morphological similarity.

The taxonomic history of the subfamily is complex, and some currently accepted subfamilies of Ichneumonidae have already been classified as Ophioninae. With changes in the classifications of these subfamilies, some inconsistencies have accumulated in the Ophioninae classification, which are gradually being clarified with the aid of robust reviews and phylogenetic analyses. The most relevant large-scale taxonomic review (without phylogenetic analyses) was done by Townes (1971), who organized the subfamily in 34 genera, divided into two tribes, Ophionini (14) and Enicospilini (20).

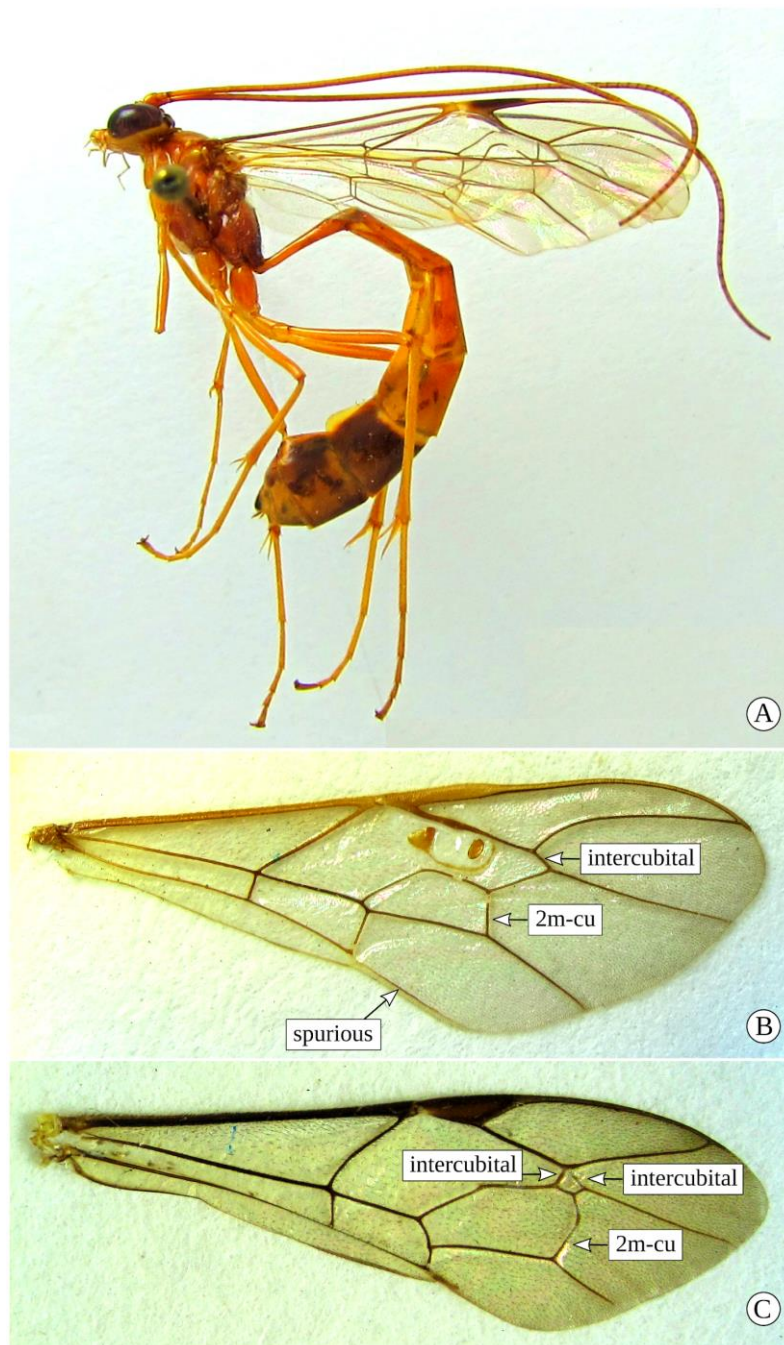


Figure 2. A. *Rhopalophion* sp. (Ophioninae), adult female, habitus; B. *Enicospilus* (Ophioninae) forewing, showing the spurious vein and the single intercubital vein, which is distad of 2m-cu vein; C. Pimplinae forewing, showing two intercubital veins, one basad and the other distad of 2m-cu vein, and without spurious vein.

Phylogenies

There are seven phylogenetic reconstructions concerning the Ophioninae genera (Table 1). Gauld (1980) used 59 characters to analyse a set of 15 genera (14 genera of Ophionini *sensu* Townes 1971, plus *Riekophion* Gauld, 1977), resulting in his *Ophion* genus-group, comprising 12 genera (four new genera and seven new synonyms). Gauld (1985) used 64 characters to analyse a set of 29 genera (20 genera of Enicospilini *sensu* Townes 1971 plus 9 genera of his *Ophion* genus-group). He used his results to propose a classification of the entire subfamily, divided into five genus-groups, with 32 valid genera (highlighting the acceptance of some paraphyletic genera). The *Ophion* genus-group *sensu* Gauld (1980) was divided into three (*Ophion*, *Sicophion* and *Eremotylus* genus-groups), while the Enicospilini *sensu* Townes (1971) was divided into two groups (*Thyreodon* and *Enicospilus* genus-group). Bennett (2004) used 64 characters to analyse the Ophioninae of Hawaii, recovering *Enicospilus* paraphyletic to respect of *Abanchogastra*, *Banchogastra* and *Pycnophion* (all genera were posteriorly synonymized under *Enicospilus* by Bennett 2008). Gauld and Janzen (2004) used 73 characters to analyse four of the five genera included in the *Thyreodon* genus-group *sensu* Gauld (1985), corroborating some synonymies proposed by Townes and Townes (1966). Quicke *et al.* (2005) used molecular data and 67 morphological characters to perform an analysis of Campopleginae using 11 Ophioninae genera as outgroups and found intriguing results, recovering among the Ophioninae two aberrant Campopleginae genera, *Skiapus* Morley,

1917 and *Hellwigia* Gravenhorst, 1823. Although with few Ophioninae genera and species included, without morphological support, as *Hellwigia* and *Skiapus* have neither the ophionoid facies nor the characteristic forewing venation, and without including the type species of both genera in the analysis, Quicke *et al.* (2005) transferred them both to Ophioninae. Quicke *et al.* (2009) used molecular data and 162 morphological characters to perform a phylogenetic analysis of the entire family Ichneumonidae, including an expanded sampling of Ophioninae (28 genera). Unfortunately, they used rather unconventional and strongly questionable methods, and in the morphological matrix presented, Ophioninae is coded as a single terminal, overlooking generic and specific variation, but *Skiapus* sp. and *Hellwigia obscura* are presented as separate terminals. Although not recovering the Ophioninae sensu Quicke *et al.* 2005, their results are important for the understanding of subfamilies relationship. In the more recent phylogenetic analysis, Rouse *et al.* (2016) used molecular data and 62 morphological characters with a more restricted sample to reassess Ophioninae phylogeny, proposing three tribes inside the subfamily (Enicospilini, Ophionini and Thyreodonini) instead of the two tribes proposed by Townes (1971). Unfortunately their morphological matrix has some serious errors, like char. 26 with all terminals with the same state (0), or its char. 45, which has two states (0, 1), but in the matrix a state '2' appears for many terminals. Beside the matrix errors, some conclusions were not supported by their results, like the affirmation that their analysis support the monophyly of Ophioninae including *Skiapus* and *Hellwigia*, although *Hellwigia* is not included in the combined analysis.

Obviously, some of these phylogenetic analyses were hampered by the limitations of the methods chosen (or available at the time), others by the limited sample of genera or even by the characters (and states) employed. Considering all this, without disregarding the contribution of these phylogenies to understand the internal relationships of the subfamily, but focusing on the morphological evidence, Ophioninae certainly still lacks a robust phylogenetic analysis that can conglomerate a good sampling of genera (ingroup and outgroup) with morphological characters (and states) clearly defined.

Table 1. Summary of phylogenetic analysis concerning Ophioninae genera.

Author(s) and year	Data analysed*	Ophioninae Genera included**	Methods (software)
Gauld 1980	morphology (59)	12	UPGMA (?)
Gauld 1985	morphology (64)	25	Parsimony (PHYLIP)
Bennett 2004	morphology (64)	3	Parsimony (NONA)
Gauld & Janzen 2004	morphology (73)	6	Parsimony (NONA)
Quicke <i>et al.</i> 2005	morphology (67) + molecular (28S)	13	Parsimony (PAUP) / Direct Optimization (POY)***
Quicke <i>et al.</i> 2009	morphology (162) + molecular (28S)	28	Elision + Parsimony (TNT)
Rousse <i>et al.</i> 2016	morphology (62) + molecular (28S, COI)	17	Bayesian (MrBayes)

*Information in parentheses are number of characters, for morphology, and genes, for molecular data. **The number of genera included in each analysis is relative to the 32 extant genera currently recognized (Yu *et al.* 2012; Shaw and Voogd 2019). ***Quicke *et al.* (2005) used parsimony to analyse morphological data alone, and the direct optimization to analyse morphological + molecular data.

Objectives

The main objective of this study was to provide a more robust phylogenetic hypothesis for Ophioninae based on morphological characters.

Specific objectives

In order to achieve the overall objective, some secondary objectives were established:

- Include all Ophioninae genera in the analysis;
- Evaluate all previously used morphological characters (in Ophioninae phylogeny), and propose new characters;
- Clearly define some morphological terms and body references, used ambiguously in the taxonomy of Ophioninae;
- Review poorly studied genera, to improve the taxonomy of these genera and enable the determination of specific terminals.

Material and methods

Terminology

The biogeographic information mentioned here follow the propositions of Holt *et al.* (2013). The morphological terminology adopted mostly follows Gauld (1988) for external characters, Eady (1968) for sculpture and Peck (1937) for male genitalia. Terminology of wing veins and cells follows Comstock-Needham system (Fig. 3). The main positional and directional terms used in the characters are summarized here: with the body divided by a longitudinal median line (dorsal view), there are **left** and **right** halves, which apply to structures from each side, *e.g.* left leg, right antenna

(Fig.4A); in a longitudinal axis, what is closer to head is **anterior**, and what is closer to anus is **posterior** (Fig.4A); for the appendages, what is closer to body is **basal** or **proximal**, while what is further to body is **apical** or **distal** (Fig.4A); when the body is seen from a lateral, frontal or posterior perspective, what is above it is **dorsal**, and what is below it is **ventral** (Fig.4B); when there is a particular area under consideration, a **median line** divides it in an **upper** (above) and a **lower** (below) halves (Fig.4B); for the tarsal claw, the surface facing the arolium is the **internal** one, and the opposite is the **external** one (Fig. 4C–D). Pictures were taken with a digital camera attached to a binocular microscope and using a DFC295 camera attached to a Leica M205C stereomicroscope. They were treated using GIMP software (GIMP 2019). The line drawings and plates were made using freely available graphics software Inkscape 0.92.3 (Inkscape 2019).

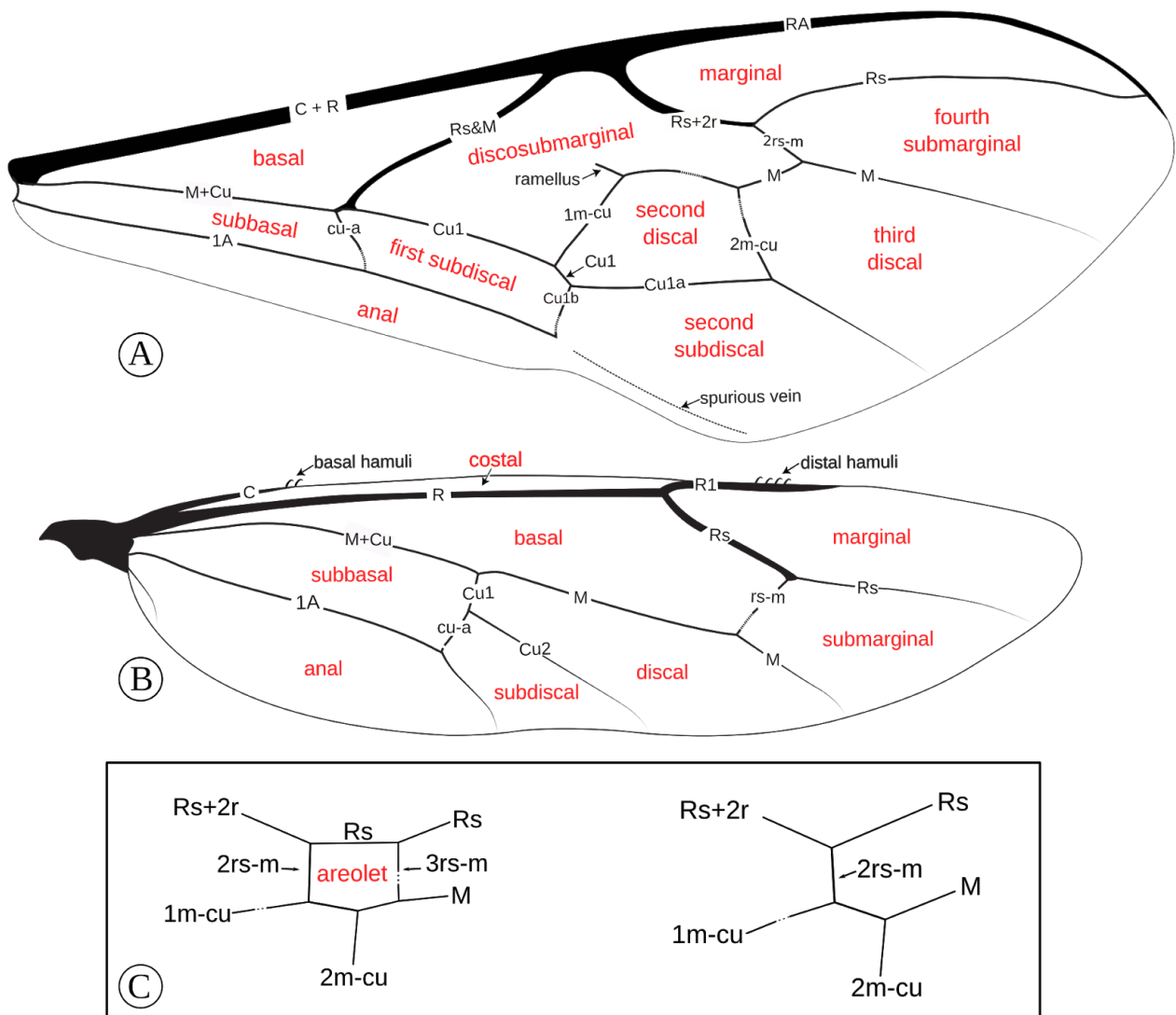


Figure 3. Schematic drawings of Ichneumonidae wings with veins (black) and cells (red). **A**, Ophioninae forewing; **B**, Ophioninae hindwing, including also basal and distal hamuli; **C**, detail of non ophionine possibilities for the areolet area, with two (left) or one (right) intercubital veins.

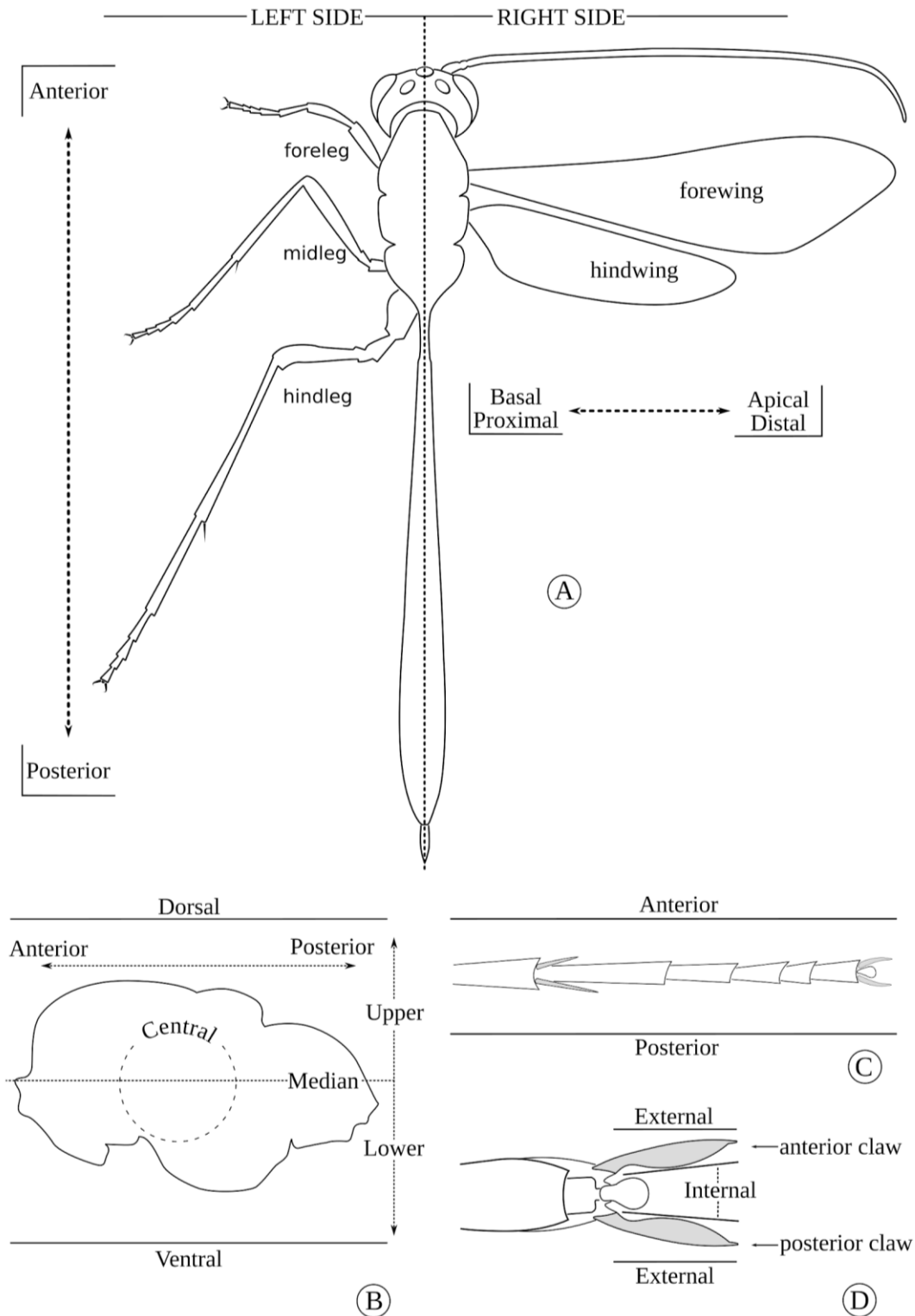


Figure 4. Schematic drawings of Ichneumonidae showing positional and directional terms. **A**, body in dorsal view, with some appendages omitted; **B**, mesosoma in lateral view, with anterior border to the left; **C**, left midleg (apex of tibia and tarsus) in ventral view; **D**, left midleg (apex of tarsus) in ventral view, with details of claws.

Taxonomic sampling

Ingroup taxa

A total of 114 Ophioninae species were examined, representing all the 32 valid genera (Yu *et al.* 2012; Spasojevic *et al.* 2018; Shaw & Voogd 2019). The species were selected in order to sample all genera, including whenever possible the type species of each genus, and a minimum number of species to contemplate as much as possible the intra-generic morphological variation along their geographic distribution (see Table 2). The original descriptions were consulted to check the identification of specimens and the range of some characters.

Table 2. The Ophioninae genera with biogeographic distribution and number of valid and examined species.

Genera	Distribution	Number of species*	Included species**
<i>Afrophion</i>	rotropical	2	1
<i>Agathophiona</i>	Nearctic	1	1
<i>Alophophion</i>	Neotropical	49	2
<i>Barytatocephalus</i>	Palaearctic	5	1
<i>Dicamptus</i>	Afrotropical; Australian; Madagascar; Palaearctic; Sino-Japanese; Oceanian; Oriental	32	5
<i>Dictyonotus</i>	Afrotropical; Madagascar; Oriental; Palaearctic; Sino-Japanese	4	2
<i>Enicospilus</i>	Afrotropical; Australian; Madagascar; Nearctic; Neotropical; Palaearctic; Panamanian; Oceanian; Oriental; Saharo-Arabian; Sino-Japanese	703	29
<i>Eremotylus</i>	Palaearctic; Nearctic; Neotropical; Saharo-Arabian; Sino-Japanese	16	5

<i>Euryophion</i>	Afrotropical; Oriental	8	3
<i>Heinrichiella</i>	Paelearctic	1	1
<i>Hellwigia</i>	Paelearctic; Saharo-Arabian	1	1
<i>Hellwigiella</i>	Paelearctic; Saharo-Arabian	2	1
<i>Janzophion</i>	Nearctic; Panamanian	2	2
<i>Laticoleus</i>	Afrotropical; Madagascan	11	4
<i>Lepiscelus</i>	Afrotropical	1	1
<i>Leptophion</i>	Australian; Oceanian; Oriental; Sino-Japanese	30	5
<i>Ophiogastrella</i>	Nearctic; Neotropical; Panamanian	6	2
<i>Ophion</i>	Australian; Nearctic; Neotropical; Paelearctic; Panamanian; Oceanian; Oriental; Saharo-Arabian; Sino- Japanese	138	16
<i>Orientospilus</i>	Afrotropical; Madagascan; Oriental	4	2
<i>Pamophion</i>	Australian	1	1
<i>Prethophion</i>	Neotropical; Panamanian	1	1
<i>Rhopalophion</i>	Afrotropical; Madagascan	3	1
<i>Rhynchophion</i>	Nearctic; Neotropical; Panamanian	4	2
<i>Riekophion</i>	Australian	3	2
<i>Sclerophion</i>	Oriental	2	2
<i>Sicophion</i>	Neotropical; Panamanian	3	1
<i>Simophion</i>	Nearctic; Paelearctic; Panamanian; Saharo-Arabian	4	2
<i>Skiapus</i>	Afrotropical; Paelearctic	3	3
<i>Stauropoctonus</i>	Australian; Madagascan; Neotropical; Paelearctic; Panamanian; Oceanian; Oriental; Sino-Japanese	11	4
<i>Thyreodon</i>	Nearctic; Neotropical; Panamanian	45	8
<i>Trophophion</i>	Nearctic	1	1
<i>Xylophion</i>	Australian	3	2
TOTAL		1100	114

*Number of extant valid species (based on Alvarado 2016; Yu *et al.* 2012; Lima 2018; Lima, Jacobi & Kumagai 2012, 2013; Shimizu & Lima 2018). **Numbers in bold indicate that the types species of the genus was examined.

Outgroup taxa

For the outgroup, nine species were selected from the Higher Ophioniformes clade (Fig.1): three Anomaloninae – *Anomalon sinuatum* (Morley, 1912), *Ophiopterus coarctatus* Brulle, 1846, and *Podogaster tranae* Gauld and Bradshaw, 1997; two Campopleginae – *Dusona* sp.1 and *Cryptophion guilhermoi* Gauld and Bradshaw, 1997; two Cremastinae – *Creagrura nigripes* Townes, 1971, and *Eiphosoma urgulium* Gauld, 2000; two Nesomesochorinae – *Nonnus* sp.1 and *Nonnus* sp.2. *Stethantyx lucasi* Graf, 1980 (Tersilochinae) was used for rooting the tree, as the subfamily is considered basal in the clade Ophioniformes (Quicke 2014).

Collections

The 536 specimens examined (Appendix 1) were obtained from nineteen institutions, listed below, organised by their acronyms, with curators or collection managers presented in parentheses (visited collections are indicated in square brackets):

AMNH – American Museum of Natural History, New York, USA (Christine LeBeau and James M. Carpenter);

BM – Bishop Museum, Honolulu, Hawaii, USA (James H. Boone);

BMNH – Natural History Museum, London, England (Gavin Broad)
[visited];

CAS – California Academy of Sciences, San Francisco, California, USA
(Robert L. Zuparko);

CCT–UFMG – Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (Fernando Silveira) [**visited**];

CZPB – Coleção Zoológica Professor Paulo Bührnheim, Universidade Federal do Amazonas, Manaus, Brazil (Fabio S. P. Godoi);

DZUP – Coleção Entomológica Padre Jesus S. Moure, Universidade Federal do Paraná, Curitiba, Brazil (Gabriel A. R. Melo) [**visited**];

FMNH – Field Museum of Natural History, Chicago, Illinois, EUA (Rebekah S. Baquiran);

INPA – Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (Márcio L. Oliveira);

LIBES – Laboratory of Insect Biodiversity and Ecosystem Science, Kobe University, Kobe, Japan (So Shimizu);

MCN – Museu de Ciências Naturais PUC Minas, Belo Horizonte, Brazil (Henrique Paprocki) [**visited**];

MIIZ – Museum and Institute of Zoology, Warsaw, Poland (David Schimrosczyk) [**visited**];

MPEG – Museu Paraense Emílio Goeldi, Belém, Brazil (Orlando T. Silveira);

MSNF – Museo di Storia Naturale, Firenze, Italy (Luca Bartolozzi);

UNESP – Universidade Estadual Paulista "Júlio de Mesquita Filho", São José do Rio Preto, Brazil (Fernando Noll) [**visited**];

UFLA – Coleção Entomológica da Universidade Federal de Lavras, Minas Gerais, Brazil (Brígida de Souza);

UFRJ – Laboratório de Entomologia da Universidade Federal do Rio de Janeiro (Daniela Maeda Takiya) [**visited**] [the 102 Ophioninae specimens found in this collection were donated to CCT–UFMG];

SMNH – Swedish Museum of Natural History Stockholm, Sweden (Hege Vårdal);

ZMHB – Museum für Naturkunde, Humboldt–Universität, Berlin, Germany (Michael Ohl) [**visited**].

Character circumscription

The structure used for character descriptions follows Sereno (2007). All the 551 morphological characters presented in the previous phylogenies concerning Ophioninae (Bennett 2004; Gauld 1980, 1985; Gauld & Jansen 2004; Quicke *et al.* 2005, 2009; and Rouse *et al.* 2016) were reevaluated to inclusion in this analysis. The generic reviews were also consulted as they are valuable sources of potentially useful phylogenetic characters (Alvarado 2014; Bennett 2008; Cushman 1944, 1947; Fernández-Triana 2005; Gauld 1977, 1988; Gauld & Mitchell 1978, 1981; Hooker 1912; Lima 2018; Lima *et al.* 2012, 2013; Morley 1912, 1917; Perkins 1915; Porter 1984; Rouse & van Noort 2014; Shimizu & Lima 2018; Townes 1971; Villemant *et al.* 2012).

Morphological external characters were studied in dried specimens, mostly at UFMG using a Leica M125 stereomicroscope, but also with equivalent stereomicroscopes at BMNH, ZMHB and MIIZ.

For ratio characters (discrete and continuous), all measurements were taken considering the linear distance between the two points of reference. As

showed by Mongiardino Koch *et al.* (2015), the choice of the ratio elements (numerator and denominator) affects the result of the analysis, potentially leading to very different phylogenetic hypotheses when alternative schemes for ratio characters are used. In order to reduce or even avoid this influence, ratios were standardized with a log-transformation [$\text{Log}_{10}(x+1)$], which was proved to be the best strategy to deal with this problem (Mongiardino Koch *et al.* 2015). After log-transformation, variation for each terminal was coded using the mean of values.

When extraction of male genitalia was permitted, it was removed from selected specimens after 24 hours in a relaxing chamber, using fine pins and forceps. The genitalia were treated for the maceration of soft tissues using a Trypsin Solution adapted from a protocol used by herpetologists for diaphanization (30mL of saturated borax solution + 70mL of distilled water + 0.5g Trypsin).

Phylogenetic analysis

The characters were coded using the Google Sheets editor. Data were then exported to text and adapted to the “.ss” matrix format, using the Linux text editor Xed ver. 2.0, keeping continuous and discrete characters in two different blocks. Data were analysed using TNT ver. 1.5 (Goloboff *et al.*, 2003; Goloboff & Catalano 2016) under equal weighting scheme. The discrete characters were treated as non-additive (= unordered), and terminals with inapplicable states were coded as “-”, and those with unobserved states as “?”. The continuous characters are always read as additive (= ordered) by TNT (Goloboff *et al.*, 2006), so inapplicable states were coded as “?”. The TNT

References

- Alvarado M. 2014. Revision of the South American wasp genus *Alophophion* Cushman, 1947 (Hymenoptera: Ichneumonidae: Ophioninae). *Revista peruana de biología*, 21(1): 3–60. doi: <http://doi.org/10.15381/rpb.v21i1.8245>
- Alvarado, M. 2016. A remarkable new species of *Sicophion* Gauld, 1979 (Hymenoptera: Ichneumonidae) from Peru, with a key to the species. *Zootaxa*, 4138(1): 195–200.
- Ashmead, W. H. 1900. "Classification of the ichneumon flies, or the superfamily Ichneumonoidea." *Proceedings of the United States National Museum*. 23 (1206):1–220. <https://doi.org/10.5479/si.00963801.23-1206.1>
- Basibuyuk, H. H. & Quicke, D. L. J. 1997. Hamuli in the Hymenoptera (Insecta) and their phylogenetic implications. *Journal of Natural History*, 31(10): 1563–1585. <https://doi.org/10.1080/00222939700770831>
- Bennett, A. M.; Cardinal, S.; Gauld, I. D. & Wahl, D. B. 2019. Phylogeny of the subfamilies of Ichneumonidae (Hymenoptera). *Journal of Hymenoptera Research*, (1): 1–157. <https://doi.org/10.3897/jhr.71.32375>
- Bennett, D. J. 2004. *A Cladistic Analysis of Hawaiian Ophionine Wasps (Hymenoptera: Ichneumonidae)* (Doctoral dissertation, The University of Kansas).
- Bennett, D. J. 2008. The ophionine wasps of Hawaii (Hymenoptera: Ichneumonidae). *Journal of Hymenoptera Research*, 17(1): 1–43.
- Bremer, K. R. 1994. Branch support and tree stability. *Cladistics*, 10(3): 295–304. <https://doi.org/10.1111/j.1096-0031.1994.tb00179.x>
- Broad, G. R., Shaw, M. R., & Fitton, M. G. 2018. Ichneumonid wasps (Hymenoptera: Ichneumonidae): their classification and biology. Royal Entomological Society, *handbooks for the identification of british insects*, 7(12). Field Studies Council.
- Cushman, R. A. 1944. The Hawaiian species of *Enicospilus* and *Abanchogastra* (Hymenoptera: Ichneumonidae). *Proc Hawaiian Entomol Soc*, 12: 39–56.
- Cushman, R. A. 1947. A generic revision of the ichneumon-flies of the tribe Ophionini. *Proceedings of the United States National Museum*, 96(3206): 417–482.
- Eady, R. D. 1968. Some illustrations of microsculpture in the Hymenoptera. In *Proceedings of the Royal Entomological Society of London. Series A, General Entomology*, 43(4-6): 66–72.
- Enderlein, G. 1912. Beiträge zur Kenntnis aussereuropäischer Ichneumoniden. II. Ophioninae. Der Gattung *Thyreodon* und ihre Verwandten. *Zoologischer Anzeiger*, 39: 624–632.
- Fernández-Triana, J. L. 2005. The taxonomy and biogeography of Cuban Ophioninae (Hymenoptera: Ichneumonidae). *Zootaxa*, 1007: 1–60.

- Gauld, I. D. 1976. The classification of the Anomaloninae (Hymenoptera: Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)*, 33(1): 1–135.
- Gauld, I.D. 1977. A revision of the Ophioninae (Hymenoptera: Ichneumonidae) of Australia. *Australian Journal of Zoology Supplementary Series*, 25(49): 1–112.
- Gauld, I. D. 1980. An analysis of the classification of the *Ophion* genus-group (Ichneumonidae). *Systematic Entomology*, 5(1): 59–82.
- Gauld, I. D. 1985. The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)*, 51: 61–185.
- Gauld, I. D. 1988. A survey of the Ophioninae (Hymenoptera: Ichneumonidae) of tropical Mesoamerica with special reference to the fauna of Costa Rica. *Bulletin of the British Museum (Natural History) (Entomology)*, 57(1): 1–309.
- Gauld, I. D., Godoy, C., Sithole, R. & Gómez, J. U. 2002. The Ichneumonidae of Costa Rica, 1. *Memoirs of the Entomological Institute*, 66: 1–768.
- Gauld, I. D., & Huddleston, T. 1976. The nocturnal Ichneumonoidea of the British Isles, including a key to genera. *Entomologist's Gazette*, 27(1): 35–49.
- Gauld, I. D., & Janzen, D. H. 2004. The systematics and biology of the Costa Rican species of parasitic wasps in the *Thyreodon* genus-group (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society*, 141(3): 297–351.
- Gauld, I. D. & Mitchell, P. A. 1978. The taxonomy, distribution and host preferences of African parasitic wasps of the subfamily Ophioninae. *Commonwealth Agricultural Bureaux*. Slough, England, U.K. 287 pp.
- Gauld, I. D. & Mitchell, P. A. 1981. The taxonomy, distribution and host preferences of Indo-Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae). *Commonwealth Agricultural Bureaux*. Slough, England, U.K. 611 pp.
- Gauld, I. D. & Shaw, S. R. 2006. Superfamilia Ichneumonoidea. In: Hanson, P. E. & Gauld, I. D. *Hymenoptera de la Región Neotropical*. Gainesville: *Memoirs of the American Entomological Institute*, 77: 443–525.
- Gauld, I. D. & Wahl, D. B. 2014. *Genera Ichneumonorum Nearcticae* [online]. Available from <http://www.amentinst.org/GIN/> [accessed december 2016].
- GIMP - GNU Image Manipulation Program. 2019 Available online: <https://www.gimp.org/> (accessed on january 2019).
- Goloboff, P. 1993. Estimating character weights during tree search. *Cladistics*, 9: 83–91.
- Goloboff, P. A. & Catalano, S. A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32(3): 221–238. <https://doi.org/10.1111/cla.12160>

- Goloboff, P.; Farris, S. & Nixon, K. 2003. TNT (Tree analysis using New Technology) version 1.5 Published by the authors, Tucumán, Argentina. Available in: <http://www.lillo.org.ar/phylogeny/tnt/>. Accessed in: 26.december.2018.
- Goloboff, PA, Mattoni, CI & Quinteros, AS. 2006. Continuous characters analyzed as such. *Cladistics*, 22: 589– 601.
- Heraty, J.; Ronquist, F.; Carpenter, J. M.; Hawks, D.; Schulmeister, S.; Dowling, A. P. G.; Murray, D.; Munro, J.; Wheeler, W. C.; Schiff, N.; & Sharkey, M. J. 2011. Evolution of the hymenopteran megaradiation. *Molecular Phylogenetics and Evolution*, 60(1): 73–88.
- Holt, B. G.; Lessard, J. P.; Borregaard, M. K.; Fritz, S. A.; Araújo, M. B.; Dimitrov, D.; Fabre, P.-H.; Graham, C. H.; Graves, G. R.; Jønsson, K. A.; Nogués-Bravo, D.; Wang, Z.; Whittaker, R. J.; Fjeldså, J. & Rahbek, C. 2013. An update of Wallace’s zoogeographic regions of the world. *Science*, 339(6115): 74–78. <https://doi.org/10.1126/science.1228282>
- Hooker, C.W. 1912. The Ichneumon flies of America belonging to the tribe Ophionini. *Transactions of the American Entomological Society*, 38: 1–176.
- Inkscape Team. 2004–2019. Inkscape: A vector drawing tool. Available from: <http://www.inkscape.org> (accessed February 2019).
- Jervis, M. 1998. Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. *Biological Journal of the Linnean Society*, 63(4): 461–493. <https://doi.org/10.1111/j.1095-8312.1998.tb00326.x>
- Lima, A. R. 2018. Revision of *Hellwigiella* Szépligeti, 1905 (Hymenoptera, Ichneumonidae, Ophioninae), with revalidation of *H. nigripennis* Szépligeti, 1905. *Zootaxa*, 4433(2): 352–360. <https://doi.org/10.11646/zootaxa.4433.2.6>
- Lima, A. R.; Jacobi, C. M. & Kumagai, A. F. 2012. A key to the Neotropical species of the *Enicospilus ramidulus* species-group (Hymenoptera: Ichneumonidae: Ophioninae), with the description of a new Brazilian species. *Zootaxa*, 3409(1): 63–68.
- Lima, A. R.; Jacobi, C. M. & Kumagai, A. F. 2013. Review of the Neotropical species of *Stauropogon* Brauns, 1889 (Hymenoptera: Ichneumonidae: Ophioninae). *Zootaxa*, 3750(5): 494–514.
- Mongiardino Koch, N.; Soto, I. M. & Ramírez, M. J. 2015. Overcoming problems with the use of ratios as continuous characters for phylogenetic analyses. *Zoologica Scripta*, 44(5): 463–474. <https://doi.org/10.1111/zsc.12120>
- Morley, C. 1912. A revision of the Ichneumonidae based on the collection in the British Museum (Natural History) with descriptions of new genera and species Part I. Tribes Ophionides and Metopiides. British Museum, London. 88pp. <https://doi.org/10.5962/bhl.title.8761>

- Morley, C. 1917. On some South African Ichneumonidae in the collection of the South African Museum. *Annals of the South African Museum*, 17: 191–229.
- Nixon, K. C. 1999–2002. WinClada version ASADO 1.61. Published by the author, Ithaca, NY, USA. Disponible in: <http://www.diversityoflife.org/winclada/>. Accessed in: 26.december.2018.
- Peck, O. 1937. The male genitalia in the Hymenoptera (Insecta), especially the family Ichneumonidae. *Canadian Journal of Research*, 15d(11–12): 221–274.
- Perkins, R. C. L. 1915. XIX. On Hawaiian Ophioninae (Hymenoptera, Fam. Ichneumonidae). *Transactions of the Royal Entomological Society of London*, 62(3–4): 521–535.
- Porter, C. C. 1984. *Laticinctus* group *Thyreodon* in the northern neotropics (Hymenoptera: Ichneumonidae). *The Wasmann Journal of Biology*, 42(1–2): 40–71.
- Quicke, D.L.J. 2014. *The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology*. Wiley-Blackwell, U. K. 704 pp. <https://doi.org/10.1002/9781118907085>
- Quicke, D.; Fitton, M.; Broad, G.; Crocker, B.; Laurenne, N. & Miah, M. I. 2005. The parasitic wasp genera *Skiapus*, *Hellwigia*, *Nonnus*, *Chriodes*, and *Klutiana* (Hymenoptera, Ichneumonidae): Recognition of the Nesomesochorinae stat. rev. and Nonninae stat. nov. and transfer of *Skiapus* and *Hellwigia* to the Ophioninae. *Journal of Natural History*, 39 (27): 2559–2578.
- Quicke, D. L. J.; Laurenne, N. M.; Fitton, M. G. & Broad, G. R. 2009. A thousand and one wasps: a 28S rDNA and morphological phylogeny of the Ichneumonidae (Insecta: Hymenoptera) with an investigation into alignment parameter space and elision. *Journal of Natural History*, 43(23–24): 1305–1421.
- Rousse, P.; Quicke, D. L.; Matthee, C. A.; Lefeuvre, P. & Noort, S. 2016. A molecular and morphological reassessment of the phylogeny of the subfamily Ophioninae (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society*, 178(1): 128–148. <https://doi.org/10.1111/zoj.12405>
- Rousse, P., & van Noort, S. (2014). Afrotropical Ophioninae (Hymenoptera, Ichneumonidae): an update of Gauld and Mitchell’s revision, including two new species and an interactive matrix identification key. *ZooKeys*, 456: 59–73. <https://doi.org/10.3897/zookeys.456.8140>
- Schwarzfeld, M. D.; Broad, G. R.; & Sperling, F. A. 2016. Molecular phylogeny of the diverse parasitoid wasp genus *Ophion* Fabricius (Hymenoptera: Ichneumonidae: Ophioninae). *Systematic Entomology*, 41(1): 191–206.
- Schwarzfeld, M. D. & Sperling, F. A. 2014. Species delimitation using morphology, morphometrics, and molecules: definition of the *Ophion scutellaris* Thomson species group, with descriptions of six new species

- (Hymenoptera, Ichneumonidae). *ZooKeys*, 462, 59–114. <https://doi.org/10.3897/zookeys.462.8229>
- Schwarzfeld, M. D. & Sperling, F. A. 2015. Comparison of five methods for delimitating species in *Ophion* Fabricius, a diverse genus of parasitoid wasps (Hymenoptera, Ichneumonidae). *Molecular phylogenetics and evolution*, 93: 234–248.
- Sereno, P. C. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics*, 23(6): 565–587.
- Shaw, M. R. & Voogd, J. 2019. Notes on the biology, morphology and generic placement of “*Hellwigia*” *obscura* Gravenhorst (Hymenoptera: Ichneumonidae, Ophioninae). *Journal of Hymenoptera Research*, 69, 39. <https://doi.org/10.3897/jhr.69.33662>
- Shimizu, S., & Lima, A. R. 2018. Taxonomic revision of the genus *Stauropogon* Brauns, 1889 (Hymenoptera: Ichneumonidae: Ophioninae) in Japan. *Entomological Science*, 21(1), 34–47. <https://doi.org/10.1111/ens.12279>
- Spasojevic, T.; Broad, G. R.; Bennett, A. M. & Klopstein, S. 2018. Ichneumonid parasitoid wasps from the Early Eocene Green River Formation: five new species and a revision of the known fauna (Hymenoptera, Ichneumonidae). *PalZ*, 1–29. <https://doi.org/10.1007/s12542-017-0365-5>
- Townes, H. K. 1969. The genera of Ichneumonidae, Part 1. *Memoirs of the American Entomological Institute*, 11: 1–537.
- Townes, H. K. 1970. The genera of Ichneumonidae, Part 3. *Memoirs of American Entomological Institute*, 13: 1–307.
- Townes H. K. 1971. The genera of Ichneumonidae, Part 4. *Memoirs of the American Entomological Institute*, 17: 1–372.
- Townes, H. K. & Townes, M. 1966. A catalog and reclassification of the Neotropic Ichneumonidae. *Memoirs of American Entomological Institute*, 8: 1–366.
- Villemant, C., Yoshida, T. & Quiles, A. 2012. A new species of *Xylophion* Gauld, 1979 (Insecta, Hymenoptera, Ichneumonidae) from Vanuatu. *Zoosystema*, 34(2): 253–259. <https://doi.org/10.5252/z2012n2a3>
- Yu, D.S.; van Achterberg, C. & Horstmann, K. 2012. *Taxapad 2012, Ichneumonoidea 2011*, Ottawa, Canada. Database on flash-drive. Available from: www.taxapad.com
- Wahl, D. B. 1991. The status of *Rhimphoctona*, with special reference to the higher categories within Campopleginae and the relationships of the subfamily (Hymenoptera: Ichneumonidae). *Transactions of the American Entomological Society*, 117: 193–213.

Annex I

First page of revision of *Stauropoctonus* elaborated as part of this thesis.

Entomological Science (2017)

doi: 10.1111/ens.12279

ORIGINAL ARTICLE

Taxonomic revision of the genus *Stauropoctonus* Brauns, 1889 (Hymenoptera: Ichneumonidae: Ophioninae) in Japan

So SHIMIZU¹  and Alessandro Rodrigues LIMA²

¹Laboratory of Insect Biodiversity and Ecosystem Science, Graduate School of Agricultural Science, Kobe University, Kobe, Japan and

²Programa de pós graduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

Abstract

The Japanese species of the ichneumonid genus *Stauropoctonus* Brauns, 1889 are revised. As a result, three species are recognized. *Stauropoctonus infuscus* (Uchida, 1928) **stat. rev.**, previously synonymized with *S. bombycivorus* (Gravenhorst, 1829), is recognized as a valid species and re-described. *Stauropoctonus bombycivorus*, which has already been recorded in Japan, is also recognized and re-described based on Japanese specimens. *Stauropoctonus aurantiacus* **sp. nov.** is described based on a single male specimen from Yakushima Island, Kagoshima Prefecture, Japan. *Stauropoctonus nigrithorax* Lee & Kim, 2002 **syn. nov.** is newly synonymized with *S. bombycivorus*. Additionally, a key to the *Stauropoctonus* species and discussions on their phenology and collection methods are provided.

Key words: key, new species, nocturnal, Old world, Palearctic region.

INTRODUCTION

The ichneumonid subfamily Ophioninae Shuckard, 1840 (Hymenoptera) comprises three tribes, 31 extant genera and over 1,100 valid species distributed in all zoogeographical regions except for the Arctic and Antarctic regions (Yu *et al.* 2012; Lima *et al.* 2013; Alvarado 2014; Rousse & van Noort 2014; Schwarzfeld & Sperling 2014; Shimizu & Watanabe 2015a; Rousse *et al.* 2016; Shimizu *et al.* 2016). They are known to be solitary koinobiont endoparasitoids of mainly middle- to large-sized lepidopterous larvae (e.g. families Hesperidae, Sphingidae, and Noctuidae) (Uchida 1928, 1954; Gauld & Mitchell 1981). Although some larvae of Scarabaeidae (Coleoptera) and Tenthredinidae (Hymenoptera) were reported as hosts (Thompson 1957; Townes 1971), all reliable records of their hosts are only from Lepidoptera

(Shimizu *et al.* 2016). Most ophionine wasps have characteristic body adapted to nocturnal habits, the “ophionoid facies” (Gauld & Huddleston 1976), and are attracted by light, like many other nocturnal ichneumonoid wasps (e.g. Townes 1971; Gauld & Mitchell 1981; Short *et al.* 2006; Quicke 2015), being considered crepuscular or nocturnal (e.g. Short *et al.* 2006; Quicke 2015; Shimizu & Watanabe 2015a; Shimizu & Maeto 2016; Shimizu *et al.* 2016).

The ophionine genus *Stauropoctonus* Brauns, 1889 comprises 11 valid species and is distributed in the Afrotropical, Australasian, Neotropical, Oriental, and Palearctic regions (Gauld & Mitchell 1981; Yu *et al.* 2012; Lima *et al.* 2013). Their biology is almost unknown, although they are expected to be solitary koinobiont endoparasitoids of lepidopterous larvae, with some host records of large-sized lepidopterous species such as the notodontid lobster moth (Uchida 1928, 1951; Gauld & Mitchell 1981).

Only *Stauropoctonus bombycivorus* (Gravenhorst, 1829) has been reported in Japan (Uchida 1928, 1951; Townes *et al.* 1965; Gauld & Mitchell 1981). *Stauropoctonus bombycivorus* was described by Gravenhorst (1829) as *Ophion bombycivorus* and was subsequently transferred from *Ophion* to *Stauropoctonus* by Brauns (1889). Uchida (1928)

Correspondence: So Shimizu, Laboratory of Insect Biodiversity and Ecosystem Science, Graduate School of Agricultural Science, Kobe University, Rokkodaicho 1-1, Nada, Kobe, Hyogo 657-8501, Japan.


Email: parasitoidwasp.sou@gmail.com

<http://zoobank.org/References/4428C36C-60D1-4AD4-A0C2-1B5CDA7D4B78>

Received 2 February 2017; accepted 2 July 2017.

Annex II

First page of revision of *Hellwigiella* elaborated as part of this thesis.

 Zootaxa 4433 (2): 352–360
<http://www.mapress.com/j/zt/>
Copyright © 2018 Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

<https://doi.org/10.11646/zootaxa.4433.2.6>
<http://zoobank.org/urn:lsid:zoobank.org:pub:701D0813-42FB-4A0F-835B-D7CCF6AEA230>

Revision of *Hellwigiella Szépligeti, 1905* (Hymenoptera, Ichneumonidae, Ophioninae), with revalidation of *H. nigripennis Szépligeti, 1905*

ALESSANDRO RODRIGUES LIMA

Programa de Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Brazil.
E-mail: alerolima@gmail.com

Abstract

The taxonomic history of *Hellwigiella Szépligeti* is presented with comments. *Ophion similis* (Szépligeti, 1905) is diagnosed and illustrated, with the first record for Morocco. *Hellwigiella* is redescribed and illustrated, with comments on its differentiation from *O. similis*. A key to the two valid species, *H. dichromoptera* and *H. nigripennis* **stat. rev.**, is provided.

Key words: Mediterranean Sea, parasitoid wasp, *Ophion similis*

Introduction

Hellwigiella Szépligeti is a small genus of Ophioninae restricted to the surroundings of the Mediterranean Sea. Instead of the ophionoid facies (Gauld & Huddleston 1976), the basic pattern of nocturnal Ophioninae, *Hellwigiella* has small eyes and ocelli and an aberrant black and reddish color pattern, suggesting that it may have diurnal habits, similar to other known diurnal species. According to Gauld (1980, 1985), the genus is classified in the *Eremotylus* genus-group, with *Eremotylus* and *Trophohion*, and suspected of being a derived lineage of *Eremotylus*. Alternatively, Rousse *et al.* (2016) placed *Hellwigiella* together with *Dicamptus*, *Enicospilus* and *Laticoleus*, in the tribe Enicospilini.

Besides the two conflicting phylogenetic hypotheses for the position of the genus, its taxonomic history is also confusing and full of misunderstandings.

Chronological taxonomic history

- 1886.** Description of the new species *Ophion dichromopterus* (Costa 1886).
1905. Description of the new genus *Hellwigiella*, with two new species (Szépligeti 1905): *H. nigripennis* and *H. similis*, without designation of the type species of the genus. The description of *H. similis* was based entirely on color, leaving no other possibility to differentiate between the species.
1914. Designation of *H. nigripennis* as the type species of the genus (Viereck 1914).
1926. Description of the new genus *Apatophion*, with a single new species, *A. mirsa* (Shestakov 1926).
1947. *Apatophion* is synonymised with *Hellwigiella* (Cushman 1947, in a footnote on p. 439).
1961. *Hellwigiella* is placed as a separate genus, but *Apatophion* is synonymised with *Ophion* (Viktorov 1961).
1966. *Hellwigiella similis* suspected to belong to *Ophion*, but the proposition marked with an interrogation (?), arguing that some verification is still needed (Shaumar 1966).
1971. *Apatophion* is placed as a separate genus, including *H. similis* and *Ophion buchariensis* Meyer, 1929 (Townes 1971). Townes redescribed *Hellwigiella*, pointing to the existence of a single species, *H. nigripennis*, but the illustration presented (Townes 1971: fig. 52) appears to be of *O. dichromopterus*.
1980. Gauld used morphological data to analyse the classification of a group of Ophioninae. He placed *Apatophion* as a synonym of *Ophion*. He also kept *Hellwigiella* as a separate genus, although speculating about the possibility of it being a derived lineage within *Eremotylus* (Gauld 1980).