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

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Belo Horizonte, Minas Gerais

2019

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(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

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## 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)	
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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

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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).

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## 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

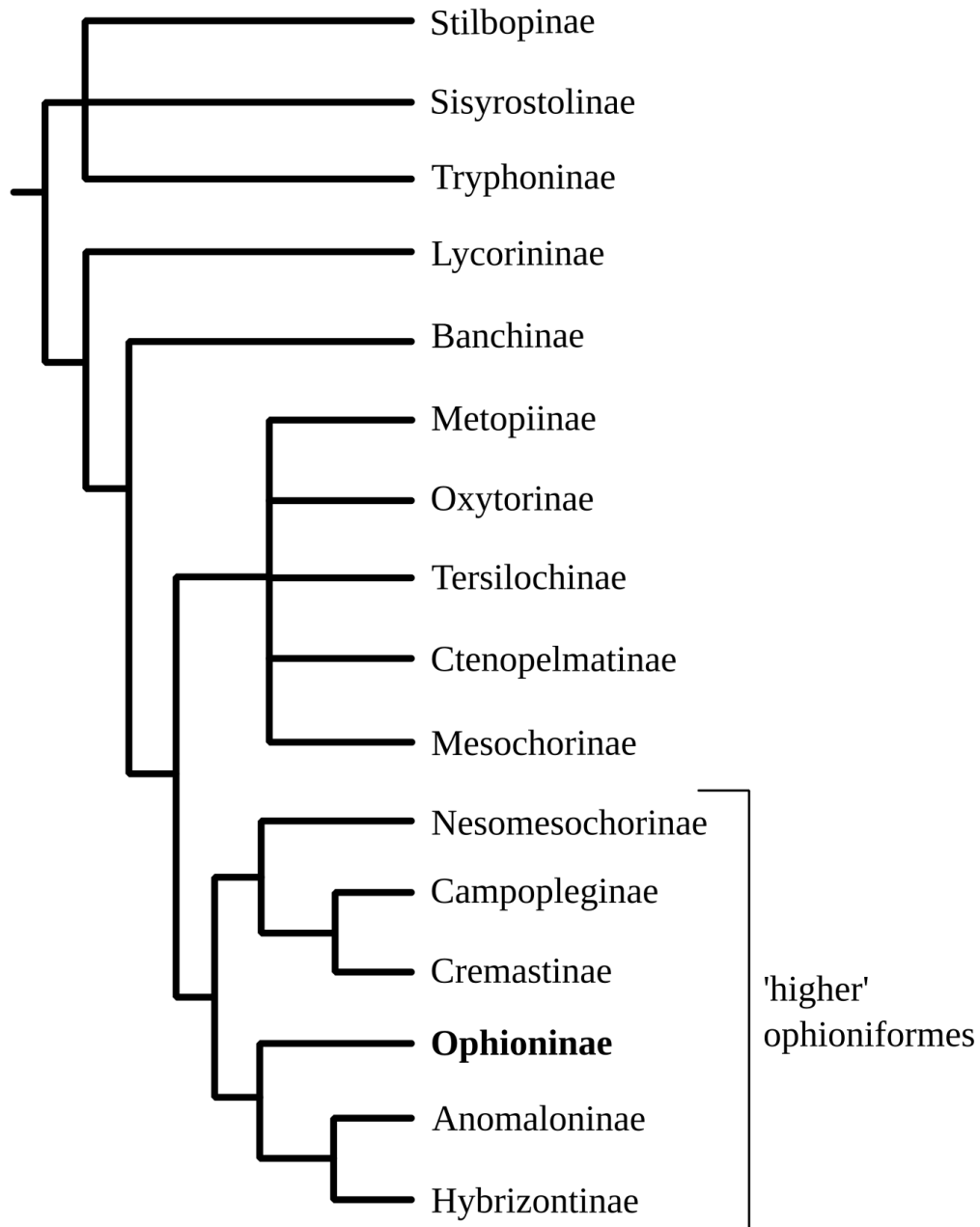
in total) were evaluated to be used. Altogether, 164 characters were employed, including some new propositions. The analysis resulted in eight equally parsimonious trees, which supported the monophyly of Ophioninae, with Campopleginae as the sister group. Inside the subfamily, the clade *Hellwigiini* **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).



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

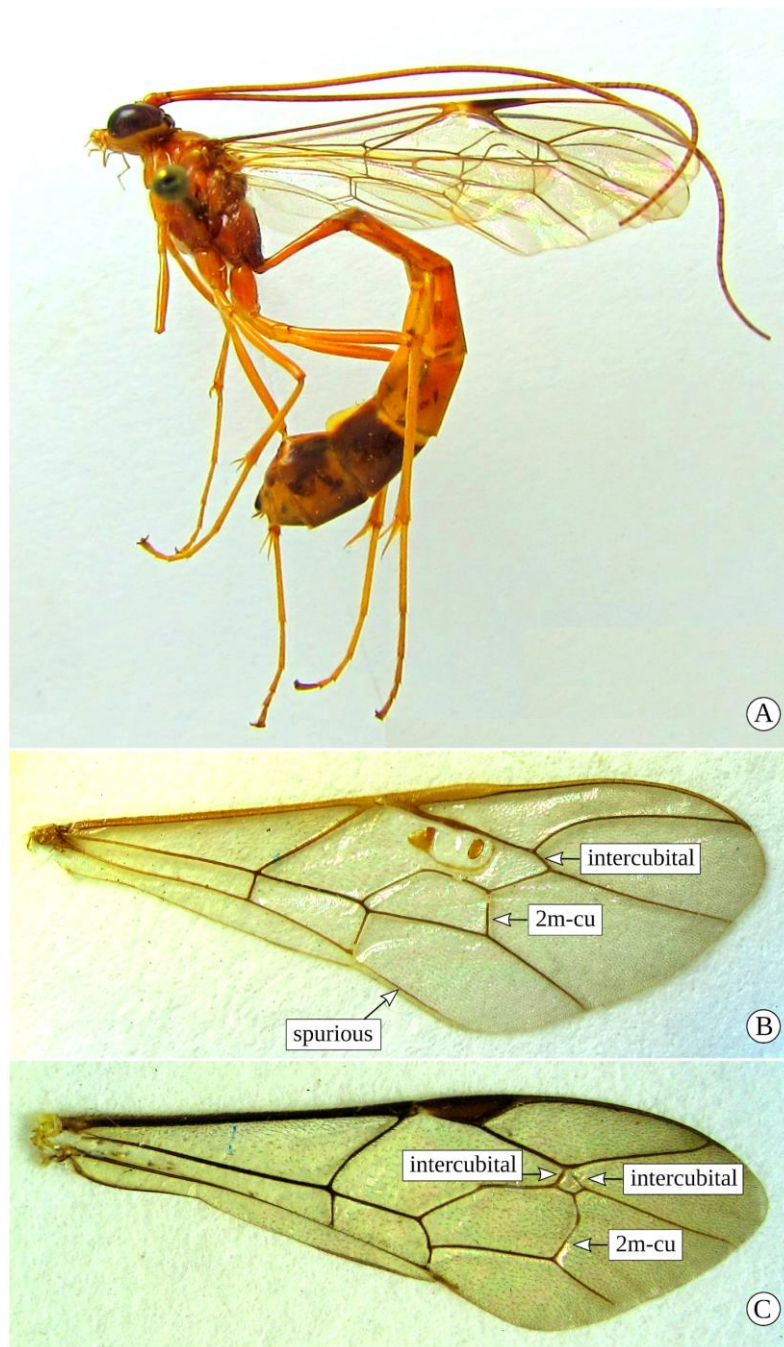
**Ophioninae Shuckard, 1840**

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.

<b>Author(s) and year</b>	<b>Data analysed*</b>	<b>Ophioninae Genera included**</b>	<b>Methods (software)</b>
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:

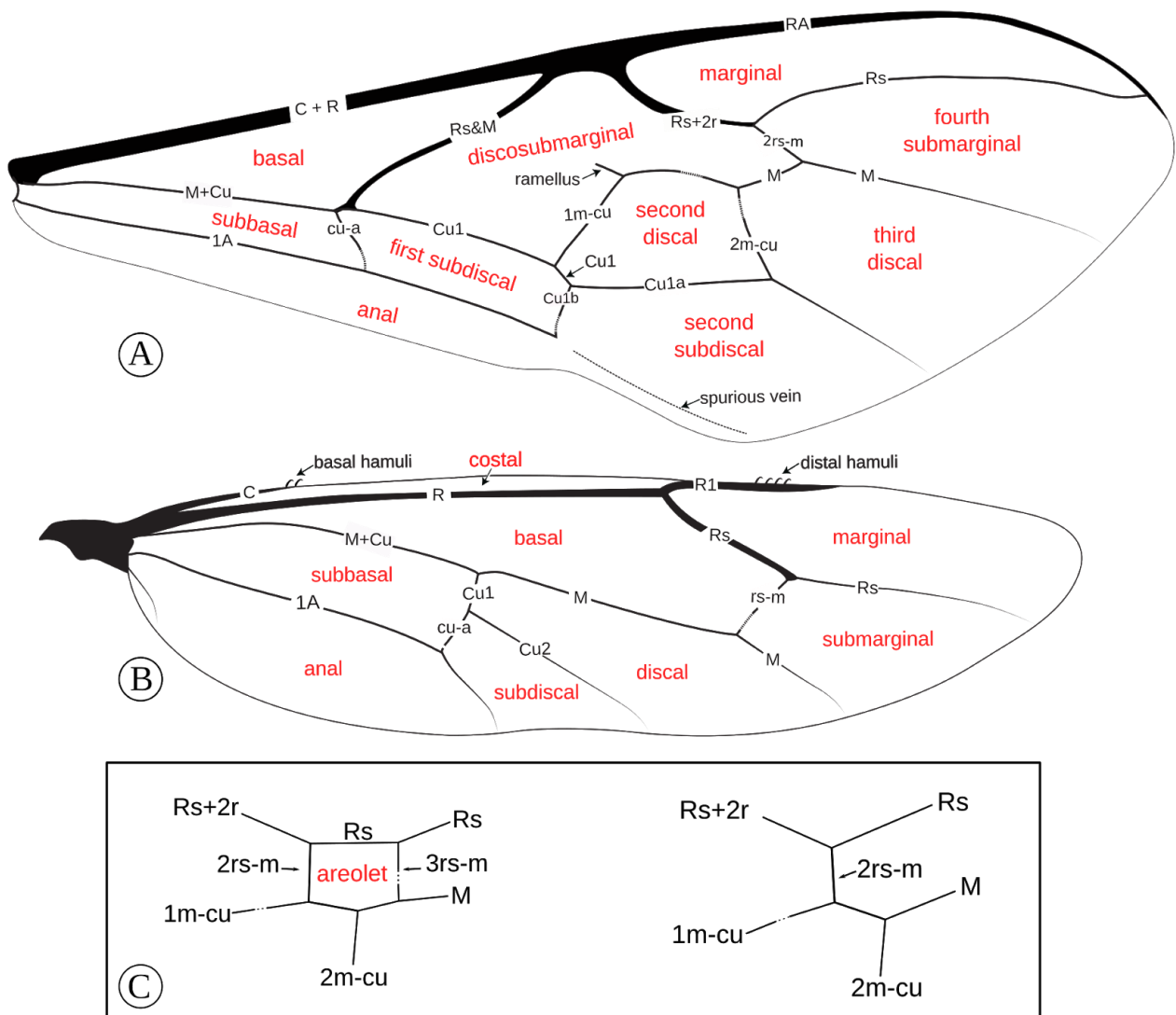
- Include all Ophioninae genera in the analysis;
- Evaluate all previously used morphological characters (in Ophioninae phylogeny), and propose new characters;
- Clearly define some morphological terms and body references, used ambiguously in the taxonomy of Ophioninae;
- Review poorly studied genera,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

## Material and methods

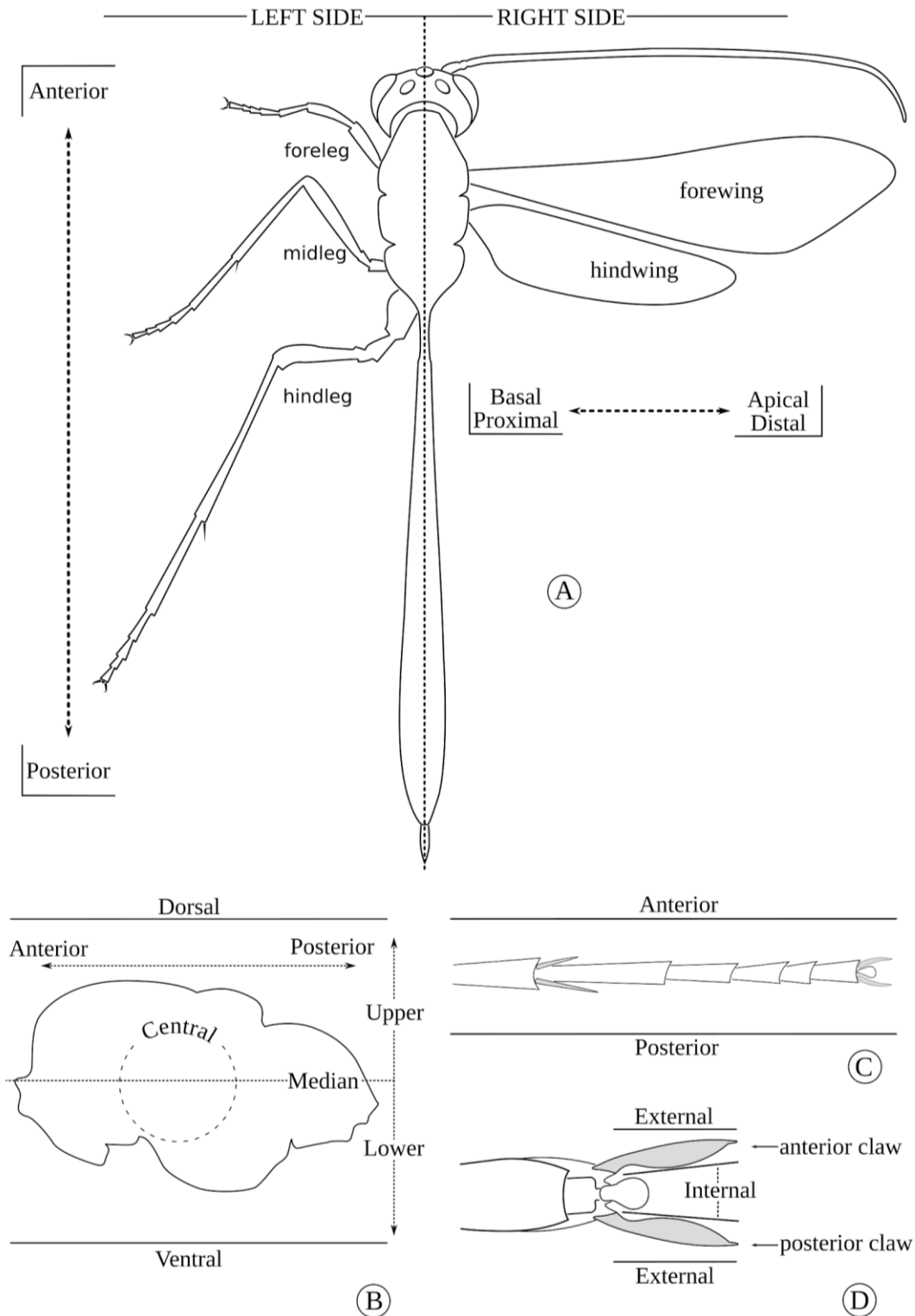
### Terminology

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.

<b>Genera</b>	<b>Distribution</b>	<b>Number of species*</b>	<b>Included species**</b>
<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>	Palaearctic	1	1
<i>Hellwigia</i>	Palaearctic; Saharo-Arabian	1	1
<i>Hellwigiella</i>	Palaearctic; 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; Palaearctic; 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; Palaearctic; Panamanian; Saharo-Arabian	4	2
<i>Skiapus</i>	Afrotropical; Palaearctic	3	3
<i>Stauropoctonus</i>	Australian; Madagascan; Neotropical; Palaearctic; 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 type 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

was run using New technology search algorithms (Sec. search + Ratchet + Drift +Tree Fusing), changing the following settings: Maximum trees held in memory: 10000; random seed 0; number of hits 100; Ratchet 200 iterations, with up-down perturbation 15; Drift 20 iterations; tree fusing 10 rounds. Support for the nodes was calculated through Bremer support (Bremer 1994) implementation in TNT. After analysis, the consensus tree was opened in Winclada software ver. 1.61 (Nixon 2002), with a matrix with discrete characters only to map state transformations, using the Unambiguous optimization scheme.

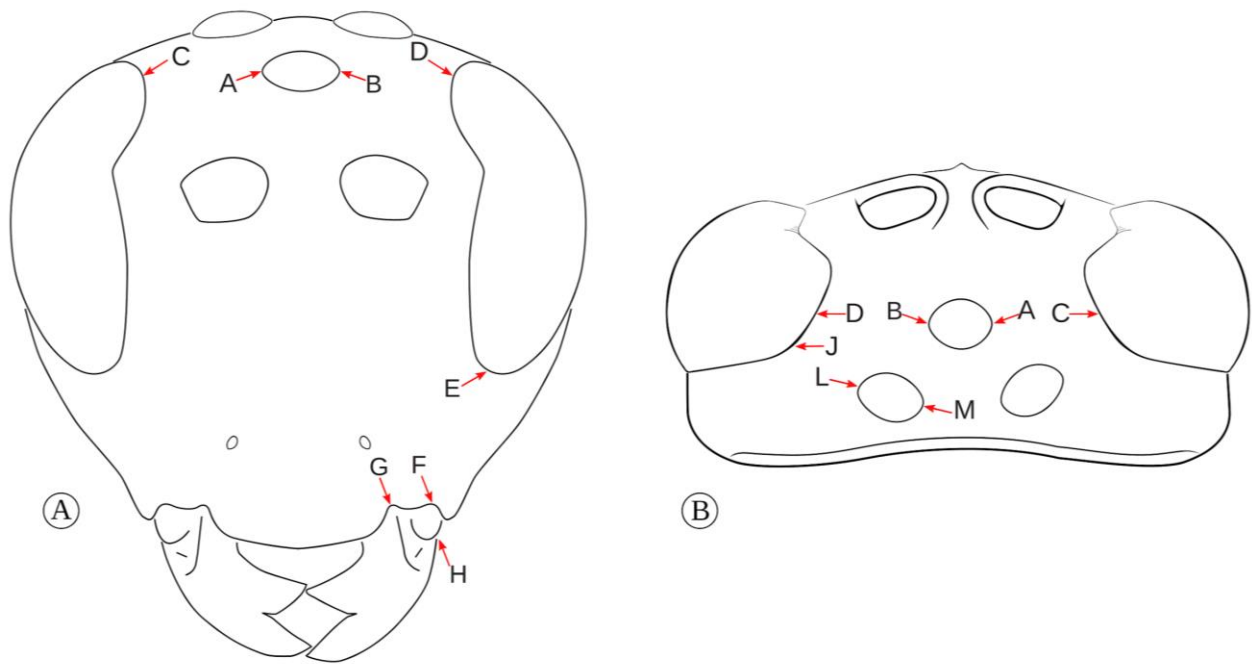
## **Results and Discussion**

### **Character list**

A total of 164 characters were circumscribed, 35 from the head, 42 from the mesosoma, 37 from wings, 28 from legs and 22 the metasoma. Altogether, 24 characters were coded with continuous states and 140 with discrete states. This is the first Ophioninae phylogeny using continuous characters coded as such. Prior to the choice of coding scheme, each ratio was measured on examined specimens (Appendix 1). Subsequently, the distributions of ratios were analyzed to verify for each character the possibility to identify distinct groups with clear and non-overlapping boundaries (i.e. clearly discernible states). All characters with clear limits were coded with discrete states. For all others, states were coded as continuous.

### ***Continuous characters***

0. Head, ratio of malar space length / basal mandibular width [Log<sub>10</sub>(x+1)] (Fig.5) [modified from Gauld 1990: char.8].
1. Head, vertex, ratio of median ocellus size / interocular distance through median ocellus (= Frontal Index) [Log<sub>10</sub>(x+1)] (Fig.5) [modified from Rouse *et al.* 2016: char.20].
2. Head, vertex, ratio of posterior ocellus distance from eye / ocellar maximum length [Log<sub>10</sub>(x+1)] (Fig.5) [modified from Gauld 1979: char.2].
3. Head, antenna, ratio of first flagellomere length (including annuli) / second flagellomere length [Log<sub>10</sub>(x+1)] [modified from Rouse *et al.* 2016: char.18].
4. Head, antenna, 20th flagellomere, ratio of its length / its apical width [Log<sub>10</sub>(x+1)] [modified from Rouse *et al.* 2016: char.19].
5. Thorax, scutellum in dorsal view, ratio of length / basal width [Log<sub>10</sub>(x+1)] [modified from Rouse *et al.* 2016: char.31].
6. Propodeum, spiracle, ratio of length of longest axis / length of the shortest axis [Log<sub>10</sub>(x+1)] [modified from Gauld 1985: char.23; Rouse *et al.* 2016: char. 34].
7. Fore leg, tarsus, ratio of 3rd tarsomere length / 5th tarsomere length [Log<sub>10</sub>(x+1)]. Length measured dorsally. All tarsomeres were measured, but the ratio between 3rd and 5th tarsomeres was more informative [new character].

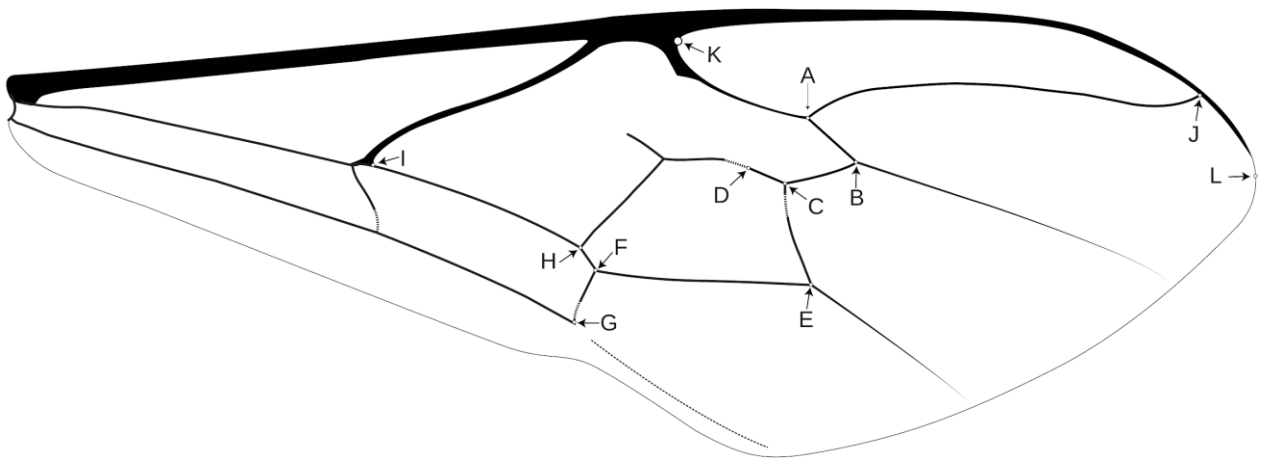


**Figure 5.** Schematic Ichneumonidae head, with points for measurement (red arrows). **A**, anterior view; **B**, dorsal view. Frontal Index (FI) = A-B / C-D; malar space length (E-F); basal mandibular width (G-H); posterior ocellus length (L-M); posterior ocellus distance from eye (J-L).

8. Hind leg, tarsus, ratio of 3rd tarsomere length / 5th tarsomere length [ $\text{Log}_{10}(x+1)$ ]. Length measured dorsally. The ratios for mid and hind legs were virtually equal, so only fore and hind legs were coded [new character].
9. Forewing, ratio of 1m-cu length (between 2m-cu and bulla) / 2rs-m length (= Alar Index) (Fig.6) [ $\text{Log}_{10}(x+1)$ ] [new character].
10. Forewing, ratio of vein 2rs-m length / abscissa of M between 2m-cu and 2rs-m (= Intercubital Index) (Fig.6). The coding of this character followed the sequence of steps below. The first step was the application of the convention: (a) for the wings with 2rs-m basad of 2m-cu, the ratio value was considered negative (Fig.7A-B); (b) for the wings with 2rs-m opposite to 2m-cu, the ratio value



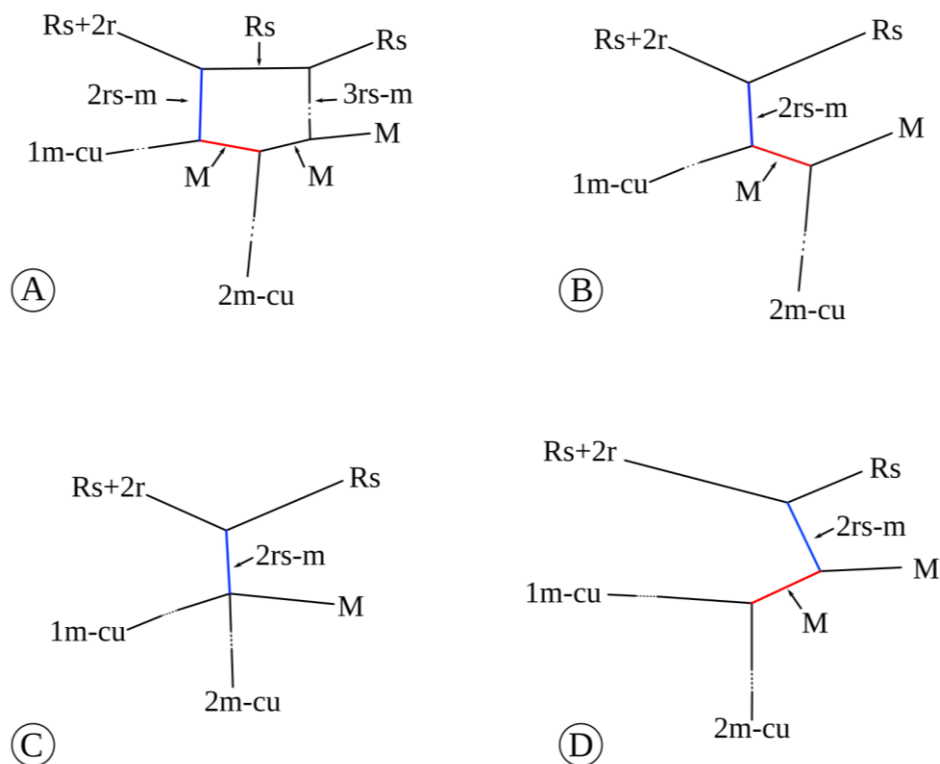
was considered equal to zero (Fig.7C); (c) for the wings with 2rs-m distad of 2m-cu, the ratio value was considered positive (Fig.7D). The second step was transformation of all the values to be positive (= equal to or greater than zero), adding the same number to all individual values so that the smallest original value for the index was turned to zero. Finally, the third step was log-transformation  $[\text{Log}_{10}(x+1)]$  [modified from Gauld 1985: char. 48.1–2].



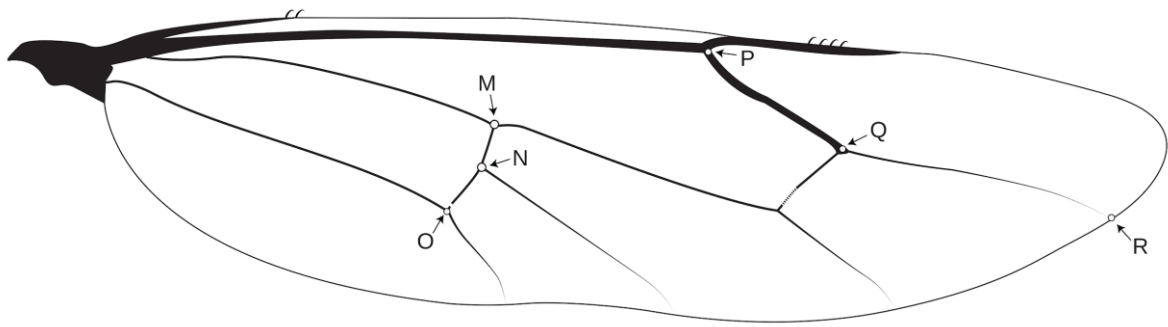
**Figure 6.** Schematic Ophioninae forewing, showing reference points for measuring of alar indexes. Alar Index (AI) =  $C-D / A-B$ ; Intercubital Index (ICI) =  $A-B / B-C$ ; Cubital Index (CI) =  $F-H / F-G$ ; Second Discoidal Index (SDI) =  $E-F / H-I$ ; Marginal Cell Index (MCI) =  $J-K / K-L$ ; Radial Index (RI) =  $A-K / A-J$ .

11. Forewing, ratio of Cu1 length (between 1m-cu and Cu1a) / Cu1b length (= Cubital Index) (Fig.6)  $[\text{Log}_{10}(x+1)]$  [new character].
12. Forewing, ratio of Cu1a length (between Cu1b and 2m-cu) / Cu1 length (between Rs+M and 1m-cu) (= Second Discoidal Index) (Fig.6)  $[\text{Log}_{10}(x+1)]$  [modified from Gauld 1985: char.37].

13. Forewing, ratio of marginal cell length / distance between base of  $Rs+2r$  and wing apex (= Marginal Cell Index) (Fig.6) [ $\text{Log}_{10}(x+1)$ ] [new character].
14. Forewing, ratio of  $Rs+2r$  length /  $Rs$  length (= Radial Index) (Fig.6) [ $\text{Log}_{10}(x+1)$ ] [New character].
15. Hindwing, ratio of  $Cu1$  length (between  $M$  and  $cu-a$ ) /  $cu-a$  length (= Nerverlar Index) (Fig.8) [ $\text{Log}_{10}(x+1)$ ] [modified from Gauld 1985: char.43.1-2].



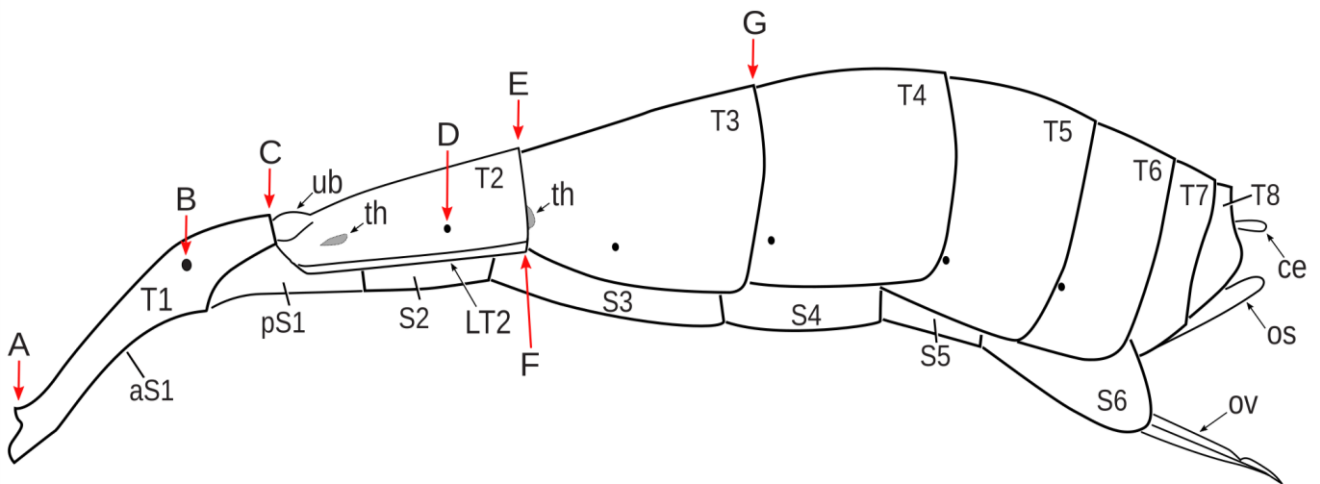
**Figure 7.** Schematic drawings of the forewing region considered to measure the Intercubital Index. **A**, two  $rs-m$  veins present (=areolet present); **B–D**, with a single  $rs-m$  vein, in different positions relative to  $2m-cu$  vein, basad, opposite and distad, respectively.



**Figure 8.** Schematic Ophioninae hindwing, showing reference points for measuring of alar indexes/ratios. Nervelar Index (NI) =  $M-N / N-O$ . Ratio of Rs vein =  $P-Q$  (basal abscissa) /  $Q-R$  (apical abscissa).

16. Hindwing, Rs vein, ratio of basal abscissa length / apical abscissa length (Fig.8) [ $\text{Log}_{10}(x+1)$ ] [new character].
17. Hindwing, anterior margin, near vein C, basal hamuli, number. [modified from Quicke *et al.* 2009: char.52].
18. Hindwing, anterior margin, on vein R1, distal hamuli, number. [modified from Rouse *et al.* 2016: char.56].
19. Metasoma, tergite I, ratio of distance from spiracle to anterior margin / tergite I length (Fig.9) [ $\text{Log}_{10}(x+1)$ ] [modified from Rouse *et al.* 2016: char.38].
20. Metasoma, ratio of tergite I length / tergite II length (Fig.9) [ $\text{Log}_{10}(x+1)$ ]. [modified from Quicke *et al.* 2009: char.81]
21. Metasoma, tergite II, ratio of distance from spiracle to anterior margin / tergite II length (Fig.9) [ $\text{Log}_{10}(x+1)$ ] [New character].
22. Metasoma, ratio of tergite II length / tergite III length (= Dorsal Metasomal Index) (Fig.9) [ $\text{Log}_{10}(x+1)$ ] [modified from Quicke *et al.* 2009: char.90].

23. Metasoma, tergite II, ratio of length / posterior width (lateral view) (Fig.9) [ $\text{Log}_{10}(x+1)$ ] [modified from Gauld 1985: char.31 = (0) longer, profile rectangular; (1) equal, profile quadrate; Rousse *et al.* 2016: char.40 = (0) less than 3x; (1) more than 3x].

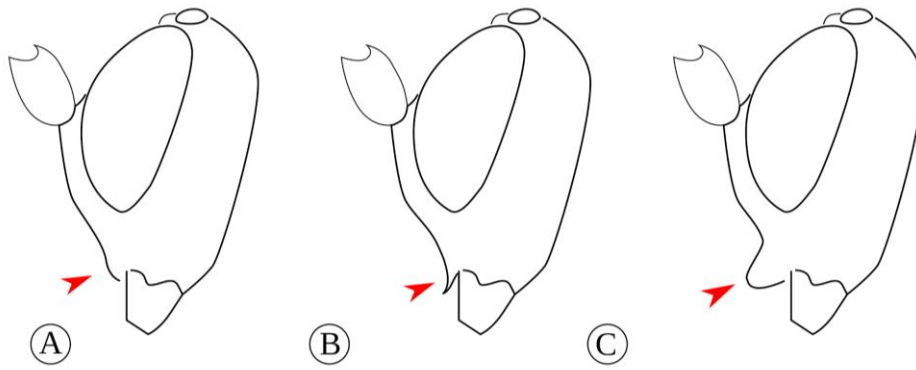


**Figure 9.** Schematic metasoma of Ophioninae, showing reference points for measuring Char. 19 = A-B / A-C; Char. 20 = A-C / C-E; Char. 21 = C-D / C-E; Char. 22 = C-E / E-G; Char. 23 = C-E / E-F. aS1 - anterior sclerotized section of first sternite; ce - cercus; LT2 - laterotergite of tergite 2; os - ovipositor sheath; ov - ovipositor; S - sternite; T - tergite; th - thyridium; ub - umbo.

### ***Discrete characters\****

\*Numbers inside square brackets are the sequential numbers of the discrete block only.

- 24[0]. Head, clypeus, shape in lateral view: (0) slightly convex to virtually flat (Fig.10A); (1) flared outwards (Fig.10B); (2) nasutiform (Fig.10C). [modified from modified from Gauld 1985: char.7.1-2].



**Figure 10.** Head in lateral view. Red arrowhead points clypeus. **A**, slightly convex; **B**, flared outwards; **C**, nasutiform.

25[1]. Head, clypeus, shape in anterior view: (0) simple, truncate to slightly convex or slightly concave; (1) centrally produced and pointed [a median tooth or teeth] (Fig.11B) [modified from modified from Gauld 1985: char.6.1–2].

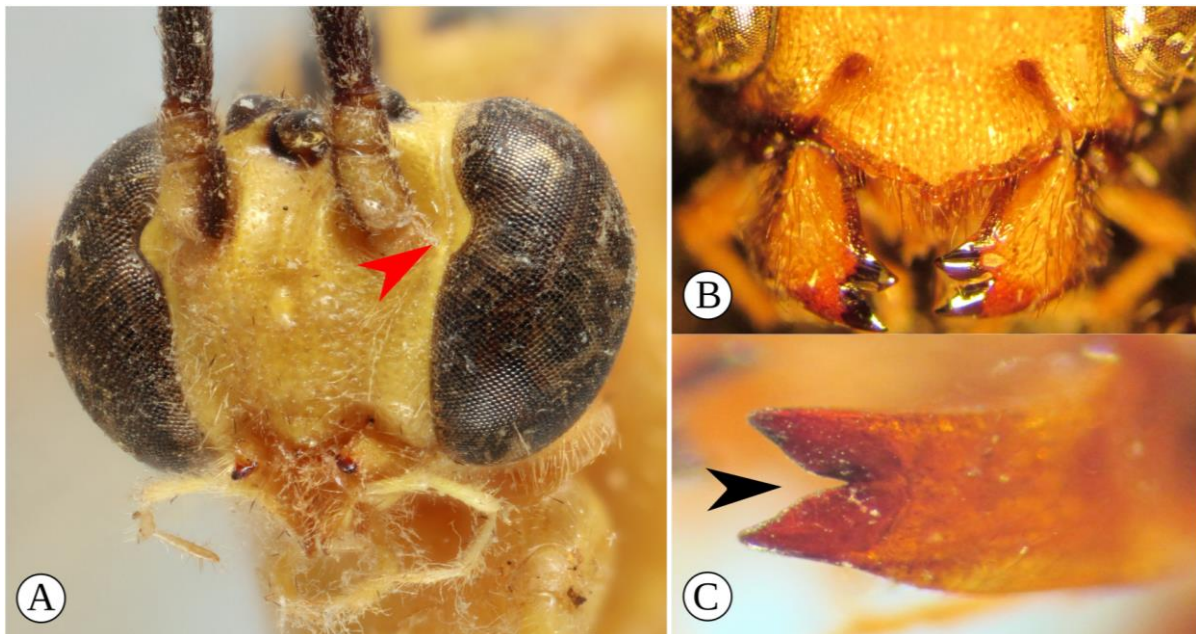
26[2]. Head, clypeus, apical fringe of closely spaced strong setae: (0) absent; (1) present (Bennett *et al.* 2019: fig.12, <https://doi.org/10.3897/jhr.71.32375.figures8-13>) [modified from Quicke *et al.* 2009: char.20].

27[3]. Head, labrum: (0) exposed (Gauld 1985: fig. 38); (1) concealed (Gauld 1985: fig. 38) [modified from Gauld & Janzen 2004: char.3].

28[4]. Head, labrum, shape: (0) flat or weakly convex; (1) strongly convex, conic. [New character].

29[5]. Head (in anterior view), compound eyes, inner margins position: (0) parallel ventrally; (1) convergent ventrally (Bennett *et al.* 2019: fig.13, <https://doi.org/10.3897/jhr.71.32375.figures8-13>) [modified from Quicke *et al.* 2009: Char.21].

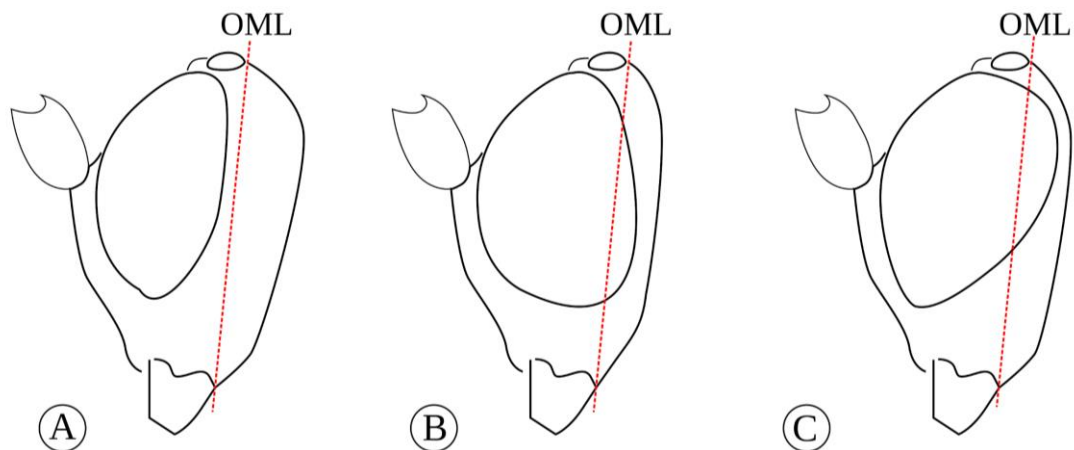
- 30[6]. Head (in anterior view), compound eyes, inner margin, emargination at level of torulli (= antennal insertion): (0) inconspicuous; (1) discernible, strong (Fig.11A) [new character].



**Figure 11.** A, *Skiapus* head in frontal view; red arrowhead points the eyes emargination at level of torulli; B, detail of clypeus in frontal view; C, mandible; black arrowhead points the triangular notch between teeth.

- 31[7]. Head (in lateral view), compound eyes, position relative to the ocellar-mandibular line: (0) not crossing the line (=entire eyes positioned anterior to the line) (Fig.12A); (1) crossing the line ventrally (Fig.12B); (2) crossing the line dorsally (Fig.12C). The ocellar-mandibular line is a virtual line running straight from posterior border of lateral ocellus to postero-ventral edge of mandibular base, with head seen in lateral view [new character].
- 32[8]. Head (in lateral view), gena, posterior margin, angle of the edge relative to the inferior portion of compound eyes: (0) convergent (narrow); (1) subparallel rounded; (2) subparallel straight [new character].

- 33[9]. Head, mandible, apex (at base of teeth), width relative to the mandibular base: (0) more than 0.5x or less as wide as; (1) 0.5x or less as wide as. [modified from Gauld 1985: char.61.1–2].
- 34[10]. Head, mandible, apex (at base of teeth), triangular notch between teeth: (0) absent; (1) present (Fig.11C) [new character].
- 35[11]. Head, mandible, basal swelling of outer surface: (0) absent, flat; (1) present. [modified from Gauld 1985: char.3; Rouse *et al.* 2016: char.7].



**Figure 12.** Head in lateral view. Red dashed line represents the ocellar-mandibular line (OML). **A**, eyes not crossing line; **B**, eyes crossing line ventrally; **C**, eyes crossing line dorsally.

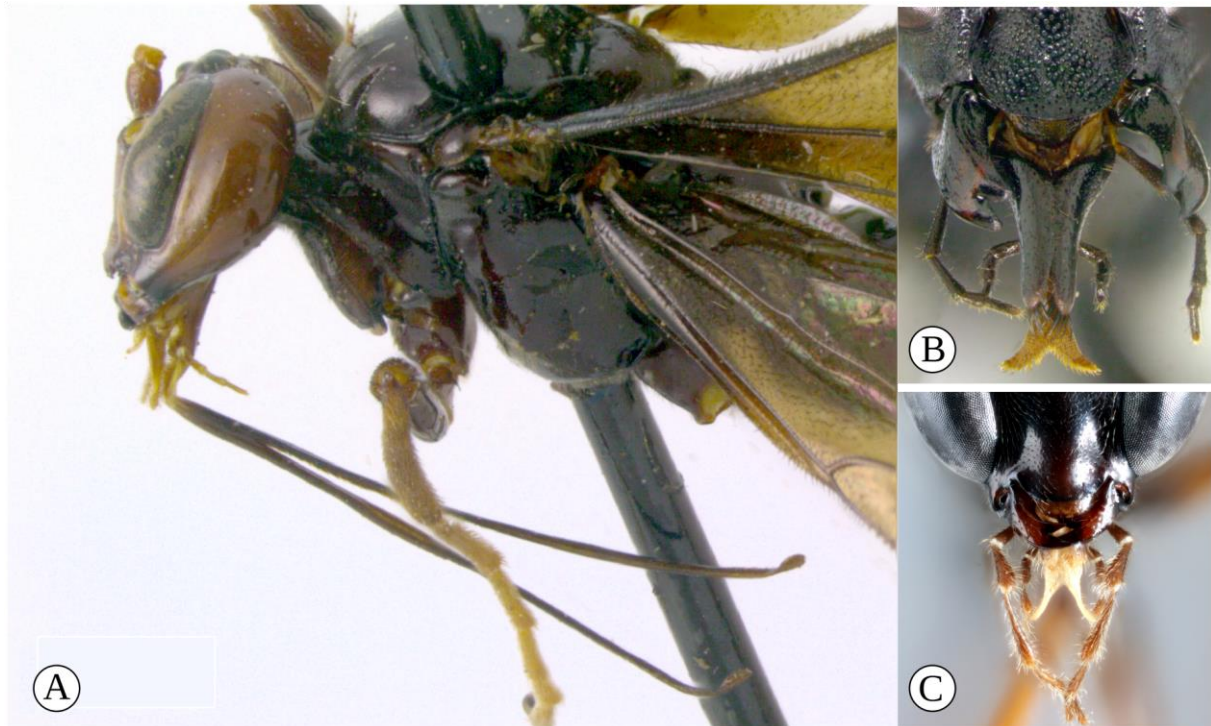
- 36[12]. Head, mandible, base, dorsal edge, sharp tooth-like lamella: (0) absent; (1) present. [new character].
- 37[13]. Head, mandible, base, ventral edge, compression: (0) not compressed; (1) moderately compressed; (2) strongly compressed, forming a translucent flange. [modified from Rouse *et al.* 2016: char.6].

- 38[14]. Head, mandible, teeth, torsion relative to the mandibular axis: (0) not torted; (1) slightly torted, with upper tooth ahead; (2) slightly torted, with lower tooth ahead; (3) strongly torted, with lower tooth ahead; (4) torted about 90°, it is not possible to define which tooth is ahead. [modified from Gauld 1985: char.5.1–2; Rouse *et al.* 2016: char.5].
- 39[15]. Head, mandible, teeth, number of teeth: (0) two conspicuous teeth; (1) two teeth, with one reduced, almost not visible when mandible is occluded (Bennett *et al.* 2019: fig.14, <https://doi.org/10.3897/jhr.71.32375.figures14-20>); (2) three or more small teeth (Shaw & Voog 2019: fig.8, <https://doi.org/10.3897/jhr.69.33662.figure8>). [modified from Rouse *et al.* 2016: char.9].
- 40[16]. Head, mandible, teeth, mid diagonal groove on outer surface covered with long setae: (0) absent; (1) present. [modified from Rouse *et al.* 2016, char. 8].
- 41[17]. Head, mandible, upper tooth, length relative to the lower tooth: (0) equal; (1) longer; (2) shorter. [modified from Rouse *et al.* 2016: char.9].
- 42[18]. Head, labiomaxillary complex: (0) unspecialized; (1) elongated glossa and galeae, with glossa concealed by galeae for most of its length (Fig.13B–C); (2) elongated glossa and galeae, with glossa reaching posterior coxae and exposed for most of its length (Fig.13A); (3) elongated glossa, galeae and maxillary palps, with



glossa exposed for most of its length. Jervis (1998) recognized seven types of specializations of labiomaxillary complex in parasitoid wasps, relating them with the extraction of floral nectar from long, narrow, tubular corollas. This syndrome was named 'concealed nectar extraction apparatus' (CNEA), and transformation series for types was postulated. The review was used to recognize the different states for the labiomaxillary complex, nonetheless they were analyzed here as non-additive states. [modified from Gauld 1985: char. 10].

- 43[19]. Head, maxillae, palps, number of segments: (0) five; (1) four; (2) three. [modified from Gauld 1985: char.8.1–2].
- 44[20]. Head, maxillae, palps, palpomere II shape: (0) cylindrical or very slightly inflate; (1) globose and inflate; (2) clavate (inflate apically); (3) grossly inflated at middle. [modified from Gauld & Janzen 2004: char.5].
- 45[21]. Head, labium, palps, number of segments: (0) four; (1) three. [modified from Quicke *et al.* 2009: char.10].
- 46[22]. Head, frons, toruli, mid longitudinal carina between toruli: (0) absent; (1) present. [modified from Rouse *et al.* 2016: char.16].
- 47[23]. Head, frons, lateral portion, sharp carinae close to and parallel with margin of eyes: (0) absent; (1) present. [modified from Gauld 1985: char.13; Gauld & Janzen 2004: char.9].
- 48[24]. Head, vertex, interocellar area, colour relative to vertex: (0) equal; (1) contrasting, black. [modified from Gauld 1985: char.59].



**Figure 13.** Labiomaxillary complex in Ophioninae. **A**, *Agathophiona*, elongated glossa and galeae, with glossa reaching posterior coxae and exposed for most of its length; **B**, *Rhynchophion*; **C**, *Sicophion*; B-C, elongated glossa and galeae, with glossa concealed by galeae for most of its length.

- 49[25]. Head, vertex, strong depression bordering posterior margin of eye: (0) absent; (1) present. [new character].
- 50[26]. Head, vertex, strong depression between occiput and occipital carina: (0) absent; (1) present. [modified from Rouse *et al.* 2016: char.21]
- 51[27]. Head, occiput, occipital carina: (0) absent; (1) present. [modified from Gauld 1980: char.1; Gauld 1985: char.1; Rouse *et al.* 2016: char.22].
- 52[28]. Head, occiput, occipital carina, extension: (0) complete, touching hypostomal carina; (1) absent laterally, not touching hypostomal carina; (2) interrupted centrally, touching hypostomal carina; (3)

interrupted centrally, and not touching hypostomal carina. [modified from Gauld 1980: char.1; Gauld 1985: char.1; Rouse *et al.* 2016: char.22].

53[29]. Head, antenna, length, relative to forewing length: (0) shorter; (1) equal or longer. [modified from Rouse *et al.* 2016: char.17].

54[30]. Thorax, pronotum, dorsal anterior margin, shape: (0) thin and flat; (1) thickened and upturned centrally; (2) strongly reflexed, the reflexed part very broad. [modified from Gauld & Janzen 2004; char.18].

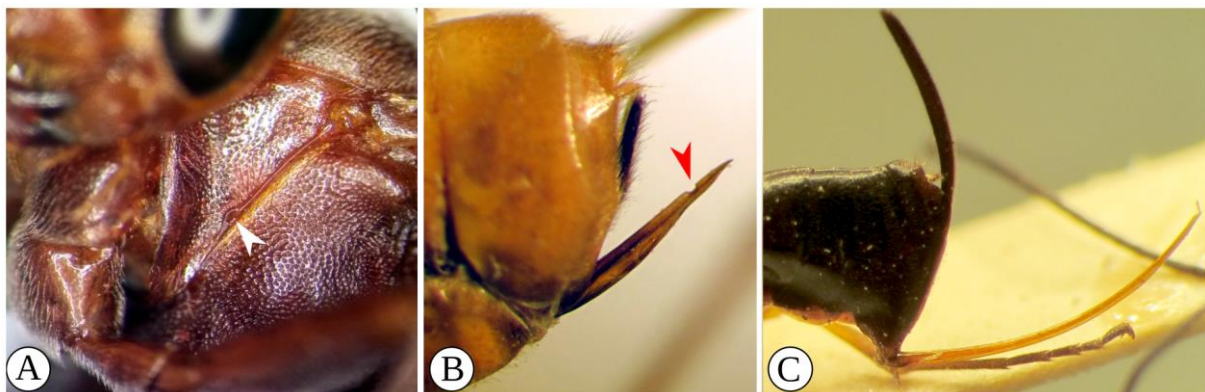
55[31]. Thorax, pronotum, dorsal surface: (0) flat to weakly convex; (1) with a shallow transverse dorsal sulcus; (2) with a narrow and deep transverse dorsal sulcus, prolonging laterally. [new character].

56[32]. Thorax, pronotum, mediodorsal area, hind margin shape: (0) thin and almost flat; (1) thickened and subquadrate in profile; (2) thickened and with upper anterior margin projecting strongly forwards; (3) projected like a hump. [modified from Gauld & Janzen 2004: char.17].

57[33]. Thorax, pronotum, lateral area, epomia: (0) absent; (1) present. [modified from Quicke *et al.* 2009: char.26].

58[34]. Thorax, pronotum, lateral area, external pit of the apodeme of occlusal spiracle muscle position: (0) on pronotum (Fig.14A); (1) between pronotum and mesopleuron (not visible). [new character].

- 59[35]. Thorax, pronotum, upper hind corner, spiracular sclerite exposure: (0) exposed; (1) concealed. [modified from Gauld 1985: char.15.1–2; Rouse et al. 2016: char.24].
- 60[36]. Thorax, propleuron, lower posterior corner, shape: (0) not produced; (1) produced as a lobe that touches or overlaps the pronotum as a posteriorly directed ventral flange. [modified from Quicke *et al.* 2009: char.29].
- 61[37]. Thorax, mesopleuron, epicnemial carina (= anterior transverse carina): (0) absent (present only on mesosternum); (1) present. [modified from Gauld 1985: char.19].
- 62[38]. Thorax, mesopleuron, sternaulus: (0) almost inconspicuous, at most with as shallow but otherwise undifferentiated depression; (1) distinctly impressed and with a sculpturally differentiated area. [modified from Gauld & Janzen 2004: char.28].



**Figure 14.** Details of morphology. **A**, *Euryophion ikuthanus*, external pit of the apodeme of occlusal spiracle muscle (white arrowhead); **B**, *Prethophion latus*, straight ovipositor, with dorsal subapical notch (red arrowhead); **C**, *Enicospilus kauaiensis*, long upcurved ovipositor.

- 63[39]. Thorax, mesopleuron, foveolar sulcus (= fovea): (0) absent; (1) present. The folveolar sulcus crosses the mesopleuron diagonally. [modified from Rouse *et al.* 2016: char.27].
- 64[40]. Thorax, mesopleuron, mesopleural furrow: (0) absent; (1) present. The mesopleural furrow crosses the mesopleuron horizontally at middle, from the episternal scrobe to its anterior margin. [modified from Gauld 1985: char.18.2; Rouse *et al.* 2016: char.27].
- 65[41]. Thorax, mesopleuron, specular groove: (0) absent; (1) present. The specular groove is a diagonal groove extending from the episternal scrobe to just below the subalar prominence, delimiting the speculum. [modified from Gauld 1985: char.18.1].
- 66[42]. Thorax, mesopleuron, lower part, sculpture: (0) finely punctate; (1) coarsely punctate; (2) smooth; (3) longitudinally striate. [modified from Gauld & Janzen 2004: char.26].
- 67[43]. Thorax, mesosternum, posterior transverse carina (= pospectal) extension: (0) complete; (1) interrupted in front of mid coxae [present medially and laterally]; (2) restricted to lateral vestiges. [modified from Gauld 1985: char.27.1–3].
- 68[44]. Thorax, mesoscutum, notaulices, extension: (0) vestigial or indistinct; (1) weakly and shallowly impressed anteriorly; (2) more sharply impressed and reaching beyond centre of mesoscutum. [modified from Gauld 1985: char.16.2; Gauld & Janzen 2004: char.21].

- 69[45]. Thorax, mesoscutum, notaulices, projection of anterior part: (0) not projected; (1) with inner margin raised to form a longitudinal ridge; (2) with a strong transverse crest. [modified from Gauld & Janzen 2004: char.23].
- 70[46]. Thorax, scutellum shape, in lateral view: (0) evenly rounded, weakly inflated; (1) strongly inflated, forming two different faces (dorsal and posterior). [new character].
- 71[47]. Thorax, scutellum, scutellar carinae: (0) absent; (1) present. [modified from Gauld 1985: char.20.1].
- 72[48]. Thorax, scutellum, scutellar carinae, extension, relative to length of the scutellum: (0) basal third; (1) between 1/3 and 2/3; (2) more than 2/3. [modified from Gauld 1985: char.20.1].
- 73[49]. Thorax, postscutellum, shape, in lateral view: (0) almost flat or weakly convex; (1) strongly inflated, projecting backwards centrally. [new character].
- 74[50]. Thorax, postscutellum, lateral carina: (0) absent; (1) present, bordering lateral margins of postscutellum. [new character].
- 75[51]. Thorax, metanotum, hind margin, shape: (0) slightly convex; (1) swollen backwards, directed to propodeal spiracle. [modified from Gauld 1985: char.21; Rouse *et al.* 2016: char.32].
- 76[52]. Thorax, metapleuron, convexity: (0) normal (weakly to moderately convex); (1) exceptionally convex near posterior

margin; (2) exceptionally inflate centrally; (3) strongly inflate (uniformly). [modified from Gauld 1980: char.26].

77[53]. Thorax, metapleuron, submetapleural carina, shape: (0) as a narrow flange, sometimes slightly more prominent anteriorly; (1) strongly produced as a broad triangular flange anteriorly. [modified from Quicke *et al.* 2009: char.39].

78[54]. Propodeum, lateral view, grossly inflated to overhang reduced metapleuron, presence: (0) absent (Gauld & Janzen 2004: fig.32); (1) present (Gauld & Janzen 2004: fig.27–31). [modified from Gauld & Janzen 2004: char.37].

79[55]. Propodeum, anterior area, transverse groove, broadness: (0) broadened medially behind postscutellum, as a semicircular concavity centrally (Gauld 1985: fig.50); (1) entirely broadened and striated (Gauld 1985: fig.51); (2) narrow and deep (Gauld 1985: fig.52). [modified from Gauld 1985: char.22.1–2].

80[56]. Propodeum, anteromedian area, shape: (0) slightly convex; (1) with an anteromedian hump. [new character].

81[57]. Propodeum, base, strongly swollen with spiracles in a deep anterior transverse through: (0) absent, not swollen; (1) present. [modified from Rouse *et al.* 2016: char.33].

82[58]. Propodeum, anterior transverse carina: (0) absent; (1) present. [modified from Gauld 1985: char.24.1–2].

- 83[59]. Propodeum, anterior transverse carina, extension: (0) complete; (1) absent laterally; (2) absent centrally. [modified from Gauld 1985: char.24.1–2].
- 84[60]. Propodeum, posterior transverse carina: (0) absent; (1) present. [modified from Gauld 1985: char.25.1–2].
- 85[61]. Propodeum, posterior transverse carina, extension: (0) complete; (1) absent centrally. [modified from Gauld 1985: char.25.1–2].
- 86[62]. Propodeum, lateral longitudinal carinae: (0) absent; (1) present. [new character].
- 87[63]. Propodeum, lateral longitudinal carinae, extension: (0) complete; (1) indistinct on area superomedia. [new character].
- 88[64]. Propodeum, lateromedian longitudinal carinae: (0) absent; (1) present. [modified from Gauld 1985: char.28.1–2].
- 89[65]. Propodeum, lateromedian longitudinal carinae, extension: (0) complete; (1) indistinct on superomedia area; (2) indistinct on area petiolar. [modified from Gauld 1985: char.28.1–2].
- 90[66]. Propodeum, median longitudinal carina: (0) absent; (1) present. [new character].
- 91[67]. Propodeum, pleural carinae: (0) absent; (1) present. [new character].
- 92[68]. Propodeum, posterior mediodorsal area, shape: (0) evenly rounded; (1) with a shallow median longitudinal furrow; (2) with



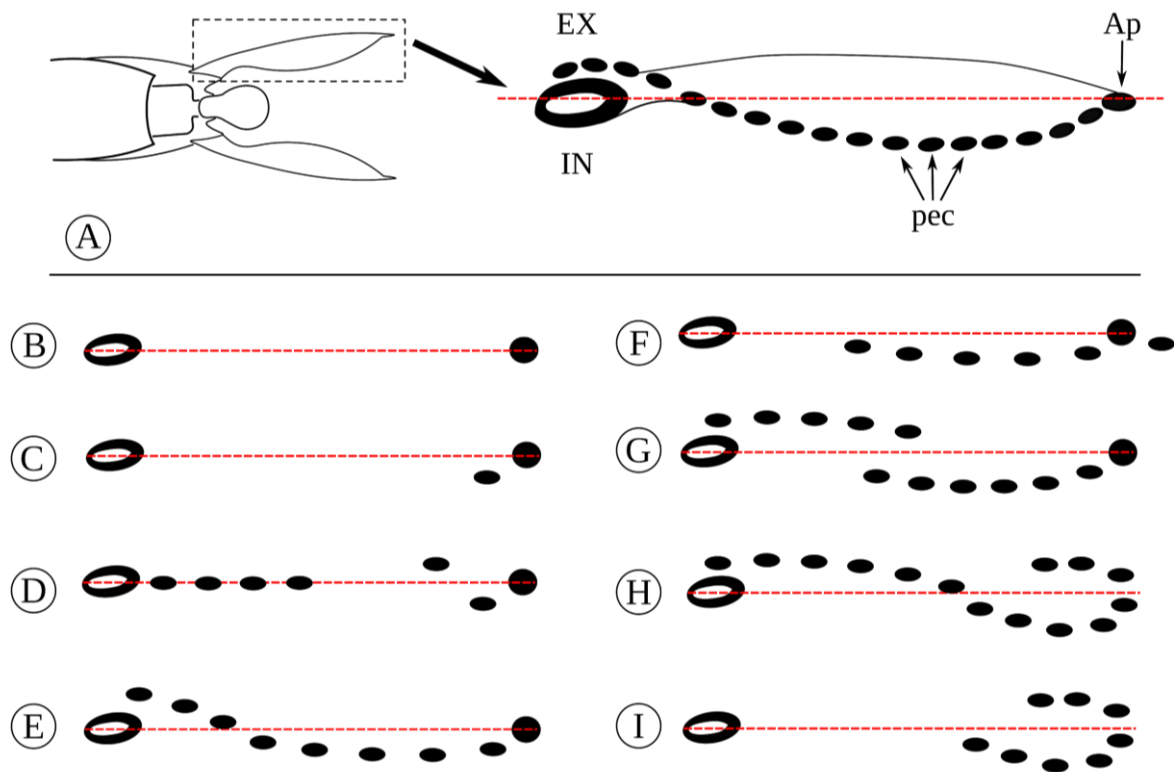
a deep median longitudinal impression. [modified from Gauld & Janzen 2004: char.42].

- 93[69]. Propodeum, propodeal spiracle, carina joining spiracle and pleural carina: (0) absent; (1) present. [new character].
- 94[70]. Fore leg, tibia, apical outer spine: (0) absent; (1) present. [new character].
- 95[71]. Fore leg, tibia, tibial spur, membranous flange behind macrotrichial comb: (0) absent (Gauld 1985: fig.49); (1) present (Gauld 1985: fig.48). [modified from Gauld 1985: char.51.1–2].
- 96[72]. Fore leg, tibia, tibial spur, membranous flange behind macrotrichial comb, length, relative to the length of macrotrichial comb: (0) virtually equal in length; (1) very reduced, 0.3x or less. [modified from Gauld 1985: char.51.1–2].
- 97[73]. Fore leg, tarsus, basal segment length, relative to the combined length of the remainder tarsomeres: (0) shorter than; (1) longer than. [new character].
- 98[74]. Mid leg, tibia, tibial spurs, length of anterior spur relative to the length of posterior one: (0) less than 0.4x as long as; (1) between 0.4x and 0.6x as long as; (2) between 0.6x and 0.8x as long as; (3) more than 0.8x as long as. [modified from Gauld 1979: char.30].
- 99[75]. Mid and hind legs, tibia, tibial apex, insertion of spurs and tarsus: (0) with common insertion for spur(s) and tarsus; (1) with

insertions of spurs and tarsus separated by a sclerotized bridge.  
[modified from Quicke *et al.* 2009: char.70].

- 100[76]. Mid leg, tibia, tibial spurs, number: (0) two; (1) one. [modified from Quicke *et al.* 2009: char.69].
- 101[77]. Hind leg, coxa, length, relative to propodeum in lateral view: (0) moderately large, its apex projecting beyond hind margin of propodeum (Gauld & Janzen 2004: fig.1); (1) small, its apex more or less level with hind margin of propodeum (Gauld & Janzen 2004: fig.2). [modified from Gauld & Janzen 2004: char.48].
- 102[78]. Hind leg, coxa, shape, in lateral view: (0) more or less globose; (1) elongate; (2) rectangular. [modified from Quicke *et al.* 2009: char.75].
- 103[79]. Hind leg, trocantellus (in lateral view), dorsal length, relative to the apical height: (0) less than apical height; (1) from 1x to 2x as long as the apical height; (2) from 2x to 3x as long as the apical height; (3) more than 3x as long as the apical height. [modified from Gauld 1979: char.16: (0) short, <0.5x as long dorsally as wide; (1) 0.6–1.2x alaw; (2) long, >1.2x alaw].
- 104[80]. Hind leg, trocantellus, distal margin, shape, in lateral view: (0) simple, convex and not projected over femur; (1) produced into a long acute down curved tooth; (2) extended as a flange over the articulation with the fêmur. [modified from Gauld 1985: chars.51.1–2 and 53].

- 105[81]. Hind leg, femur, ventral surface, median line, pilosity: (0) absent; (1) present. [new character].
- 106[82]. Hind leg, femur, ventral surface, median line, apical third, setae with apex backward curved: (0) absent; (1) present. [new character].
- 107[83]. Hind leg, tibia, anterior surface, spines-like setae along of the tibia: (0) absent; (1) present. [new character].
- 108[84]. Hind leg, tibia, tibial apex, posterior margin, comb of dense setae: (0) absent; (1) present. All setae in the comb have the same length and are inserted in a line perpendicular to the tibial axis. [modified from Quicke *et al.* 2009: char.72].
- 109[85]. Hind leg, tibia, tibial apex, inner margin, apical margin of comb, shape: (0) straight; (1) curved. [inapplicable if char.108[84] = 0] [modified from Quicke *et al.* 2009: char.73].
- 110[86]. Hind leg, tibia, posterior tibial spur, outer surface, shape, in transversal section view: (0) flattened, with a long fringe of close setae; (1) convex, with scattered setae. [modified from Gauld 1985: char.54].
- 111[87]. Fore and mid legs, tarsal claw: (0) simple (Fig.15B); (1) pectinate (Fig.15C-I). A simple tarsal claw bears a basal lobe and an acute apex. Any additional tooth is here considered as a pectinal tooth. [new character].

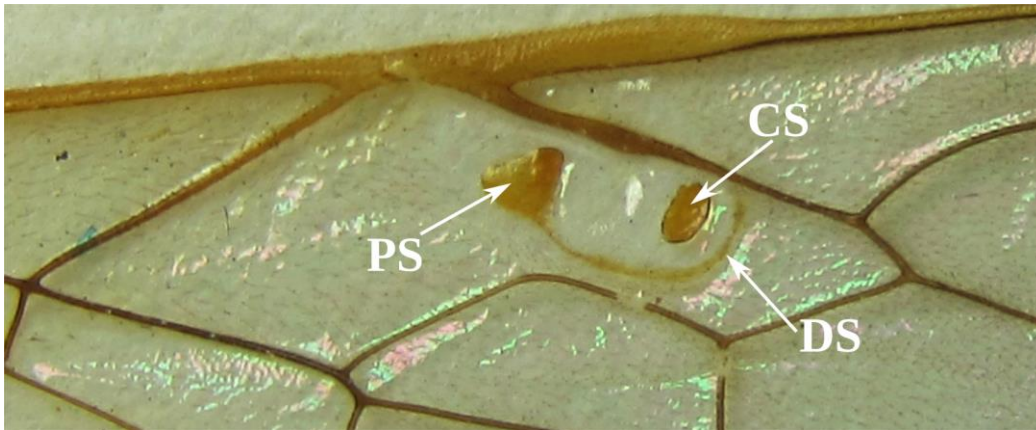


**Figure 15.** Schematic pectinal tarsal claw. Small ellipses are the pectinal comb; black circle is the acute apex of the claw; large ellipse is the basal expansion of the claw; red dashed line is the median line of the claw. **A**, apex of tarsomere five and tarsal claws in ventral view (left) and the sinuous disposition of the pectinal comb (right), running from external surface to the internal surface towards apex; **B**, simple tarsal claw (without pectinae), hind tarsal claw of *Hellwigia* and *Heinrichiella*; **C**, with a single subapical, fore/mid tarsal claw of *Hellwigia* and *Heinrichiella*, hind tarsal claw of *Skiapus*; **D**, fore/mid tarsal claw of *Skiapus*; **E**, complete sinuous pectinal comb, ost Ophioninae; **F**, pectinal comb extending beyond apex, hind tarsal claw of *Leptophion*; **G**, pectinal comb discontinued at middle, seen in *Thyreodon* and *Xylophion*; **H**, apex of tarsal claw spatulate (= not acute), surrounded by the pectinal comb, seen in *Xylophion*; **I**, similar to H, but missing the basal portion of pectinal comb, males of *Ophiogastrella*.

112[88]. Fore and mid legs, tarsal claw, pectinae: (0) reduced to a single subapical internal tooth (Fig.15C); (1) with a well-developed pectinal comb (Fig.15D–I). [inapplicable if char.111[87] = 0]. [new character].

- 113[89]. Fore and mid legs, tarsal claw, pectinae position: (0) restricted to the longitudinal midline of claw; (1) sinuous, occurring also on internal and/or external surfaces of claw (Fig.15D-I). [new character].
- 114[90]. Hind legs, tarsal claw: (0) simple (Fig.15B); (1) pectinate (Fig.15C-I). A simple tarsal claw possess a basal lobe and an acute apex. Any additional tooth is here considered as a pectinal tooth. [new character].
- 115[91]. Hind legs, tarsal claw, pectinae: (0) reduced to a single subapical internal tooth (Fig.15C); (1) with a well-developed pectinal comb (Fig.15D-I). [inapplicable if char.114[90] = 0]. [new character].
- 116[92]. Hind legs, tarsal claw, pectinae position: (0) restricted to the longitudinal midline of claw; (1) sinuous, occurring also on internal and/or external surfaces of claw (Fig.15D-I). [inapplicable if char.115[91] = 0]. [new character].
- 117[93]. Hind legs, tarsal claw, pectinae: (0) pectinal comb terminating before apex of claw (Fig.15C-E, G); (1) pectinal comb extending beyond apex (Fig.15F). [inapplicable if char.115[91] = 0]. [new character].
- 118[94]. Male, legs, tarsal claw, apex of claw: (0) acute; (1) spatulate, surrounded by a pectinal comb that prolonged until the base of claw (Fig.15H); (2) spatulate, surrounded by a pectinal comb restricted to the apex of claw (Fig.15I). [inapplicable if char.115[91] = 0]. [new character].

- 119[95]. Male, hind leg, tarsus, ventral pilosity, length and density: (0) finely and sparsely pubescent; (1) with moderately long, dense pubescence. [modified from Gauld & Janzen 2004: char.52].
- 120[96]. Forewing, transparency: (0) predominantly hyaline, at most with small infuscated areas; (1) predominantly dark infuscate, at most with small fenestra; (2) predominantly with a golden reflex, at most with small infuscated areas. [modified from Gauld & Janzen 2004: char.53].
- 121[97]. Forewing, discosubmarginal cell, anterior glabrous area (at least near pterostigma): (0) absent; (1) present. [modified from Gauld 1985: char.45].
- 122[98]. Forewing, discosubmarginal cell, anterior glabrous area, position relative to pterostigma and Rs+2r vein: (0) restricted to pterostigma; (1) along the thickest portion Rs+2r vein. [inapplicable if char.121[97] = 0] [modified from Gauld 1985: char.45].
- 123[99]. Forewing, discosubmarginal cell, anterior glabrous area, glabrous area, sclerites (Fig.16): (0) absent; (1) present. [modified from Gauld 1985: char.46].
- 124[100]. Forewing, discosubmarginal cell, anterior glabrous area, proximal sclerite (Fig.16): (0) absent; (1) present. [inapplicable if char.123[99] = 0] [modified from Rousse et al. 2016: char.47].



**Figure 16.** Detail of forewing discal cell. PS, proximal sclerite; CS, central sclerite; DS distal sclerite.

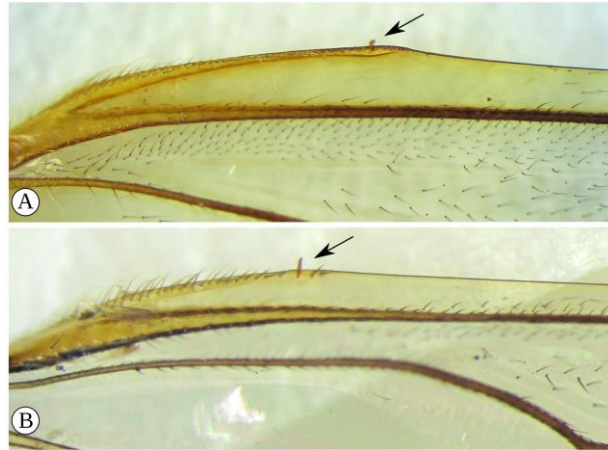
- 125[101]. Forewing, discal cell, anterior glabrous area, central sclerite (Fig.16): (0) absent; (1) present. [inapplicable if char.123[99] = 0] [modified from Rouse *et al.* 2016: char.48].
- 126[102]. Forewing, discal cell, anterior glabrous area, distal sclerite (Fig.16): (0) absent; (1) present. [inapplicable if char.123[99] = 0] [new character].
- 127[103]. Forewing, pterostigma, shape: (0) triangular, apically abruptly narrowed; (1) elongate and narrow, evenly tapered toward apex; (2) linear. [modified from Rouse *et al.* 2016, char. 51].
- 128[104]. Forewing, cross-vein 3rs-m: (0) present (= areolet closed) (Fig.7A); (1) absent (= areolet open) (Fig.7B–D). [modified from Quicke *et al.* 2009: char.47].
- 129[105]. Forewing, cell (areolet): (0) pedunculate, intercubital veins joining anteriorly before Rs vein; (1) not pedunculate, intercubital veins joining Rs vein independently. [inapplicable if char.128[104] = 1] [modified from Quicke *et al.* 2009: char.48].

- 130[106]. Forewing, 2rs-m vein, position relative to 2m-cu vein: (0) basad of; (1) opposite to; (2) distad of. [modified from Quicke *et al.* 2009: char.49].
- 131[107]. Forewing, 2rs-m vein, shape: (0) virtually straight; (1) curved (bent) near middle. [new character].
- 132[108]. Forewing, spurious vein on second subdiscal cell paralleling wing margin: (0) absent; (1) present. [modified from Rouse *et al.* 2016: char.44].
- 133[109]. Forewing, vein 1m-cu, shape: (0) angled; (1) sinuous; (2) more or less curved, without sharp angle. [modified from Rouse *et al.* 2016: char.49].
- 134[110]. Forewing, vein 1m-cu, central portion, ramellus: (0) absent; (1) present. The ramellus was only observed in specimens with forewing vein 1m-cu angled, so this character was coded applicable only for terminals with Char. 133[109] = 0. [modified from Gauld 1985: char.38].
- 135[111]. Forewing, vein cu-a, position relative to the vein Rs&M: (0) basad to; (1) opposite to; (2) distad to. [modified from Gauld 1980: char.43; Gauld 1985: char.82].
- 136[112]. Forewing, vein cu-a, inclination: (0) subvertical; (1) inclivous; (2) reclivous. [modified from Gauld 1980: char.34].
- 137[113]. Forewing, vein Rs, shape: (0) arcuate; (1) sinuous; (2) centrally dipped; (3) straight. [modified from Gauld 1980: char.49].



- 138[114]. Forewing, vein  $R_{s+2r}$  (=  $r-rs$ ), basally shape: (0) straight to curved; (1) distinctly angled (with a basal thicker straight portion, and a distal thinner portion). [modified from Gauld 1985: char.39; Rouse *et al.* 2016: char.52].
- 139[115]. Forewing, vein  $R_{s+2r}$ , central portion, shape: (0) straight; (1) sinuous; (2) bowed. [modified from Gauld 1985: char.40; Rouse *et al.* 2016: char.54].
- 140[116]. Hindwing, anterior margin, basal hamuli: (0) absent; (1) present. Although not disagreeing with the proposal of Basibuyuk and Quicke (1997), who concluded that the Ichneumonidae basal hamuli is not the true basal hamuli (exclusive from Xyelidae, Pamphiliidae and Xiphydriidae), but homologous to the secondary hamuli, the name "basal hamuli" was retained because of its widespread use in the Ichneumonidae literature. [modified from Gauld & Janzen 2004: char.62].
- 141[117]. Hindwing, anterior margin, basal hamuli insertion: (0) on vein C (Fig.17A); (1) free on membrane (Fig.17B). [inapplicable if char.140[116] = 0]. [modified from Quicke *et al.* 2009: char.53].
- 142[118]. Hindwing, hamuli on vein R1, spacing: (0) equally spaced; (1) forming at least two distinct groups. [new character].
- 143[119]. Hindwing, hamuli on vein R1, shape: (0) all hamuli equally shaped; (1) subapical hamulus thinner and longer than the others, coiled; (2) one or more basal hamuli clearly thinner than the others. [new character].

- 144[120]. Hindwing, hamuli on vein R1, position, relative to base of R1 vein: (0) first hamulus closer to second one than to base of R1 vein; (1) first hamulus close to base of R1 by at least same distance to the second hamulus. [new character].



**Figure 17.** Detail of hindwing, with position of basal hamuli (black arrow). **A**, on vein C; **B**, free on membrane.

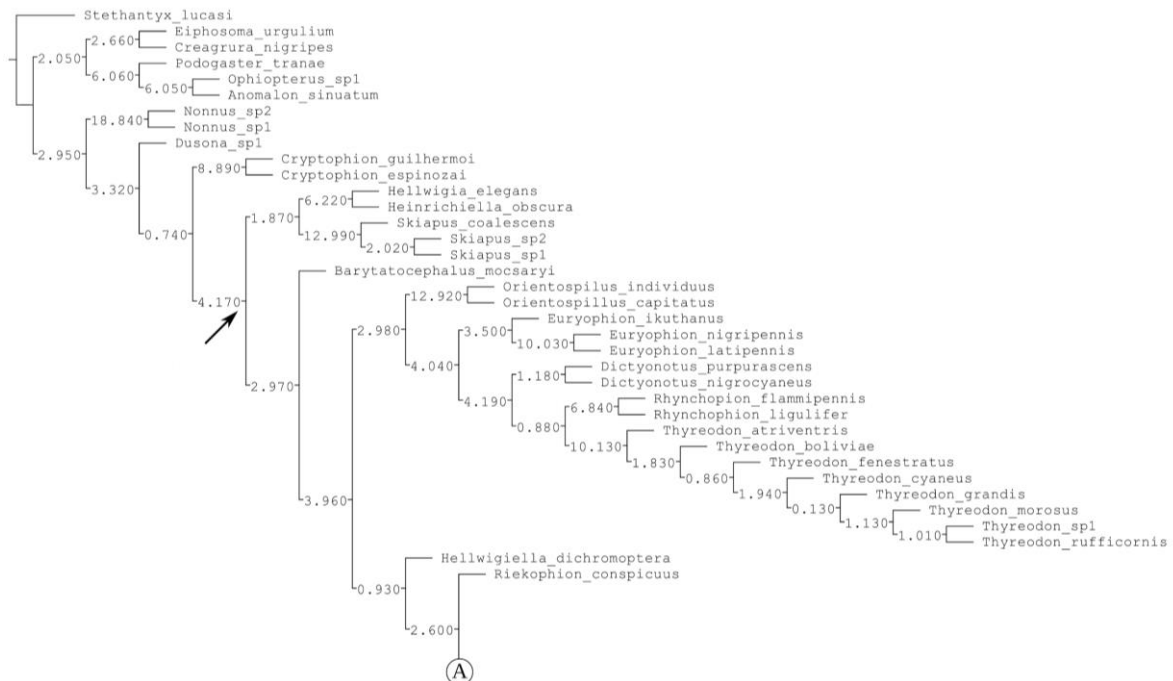
- 145[121]. Hindwing, marginal cell, anterior portion, pilosity: (0) finely and sparsely hirsute, the membrane not thickened; (1) glabrous, with membrane thickened. [modified from Gauld & Janzen 2004: char.61].
- 146[122]. Hindwing, vein Rs, first abscissa, shape: (0) almost straight to evenly concave; (1) curved basally, straight apically; (2) strongly curved; (3) sinuous (basally concave, apically convex); (4) strongly convex. [modified from Gauld 1980: char.37; Rouse *et al.* 2016: char.55].
- 147[123]. Metasoma, tergite I, glymmae: (0) absent; (1) present. [modified from Quicke *et al.* 2005: char.58].

- 148[124]. Metasoma, tergite I, spiracle, position relative to the posterior margin of the anterior sclerotised section (AS1) of sternite I: (0) anterior; (1) opposite; (2) posterior. [modified from Gauld 1985: char.32].
- 149[125]. Metasoma, tergite II, anterior margin, umbo: (0) absent; (1) present. [modified from Gauld 1985: char.33; Rouse *et al.* 2016: char.41].
- 150[126]. Metasoma, tergite II, laterotergite (epipleura), position relative to tergite: (0) folded beneath; (1) pendant. [modified from Gauld 1985: char.30].
- 151[127]. Metasoma, tergite II, thyridium: (0) absent; (1) present. [modified from Gauld 1985: char.29.1–2].
- 152[128]. Metasoma, tergite II, thyridium, distance relative to anterior margin of tergite II: (0) less than its length; (1) at least as long as its length. [modified from Gauld 1985: char.29.1–2].
- 153[129]. Metasoma, tergite III, basal thyridium: (0) absent; (1) present. [modified from Quicke *et al.* 2009: char.84].
- 154[130]. Male, genitalia, aedeagus, penisvalva, apex, side flap: (0) absent; (1) present. [new character].
- 155[131]. Male, genitalia, gonostipes, apex, inner surface, pilosity, relative to the external surface: (0) pilose; (1) glabrous. [new character].
- 156[132]. Male, genitalia, gonostipes, dorsal area: (0) basally fused; (1) not fused. [new character].

- 157[133]. Male, sternite VIII, distal margin, shape: (0) convex to straight; (1) projected into a medial upward pointed tip; (2) with an internal pointed projection; (3) concave; (4) trapezoidal, with four long robust spine-like setae. [new character].
- 158[134]. Female, metasoma, tergite II, crease at least partly separating laterotergite: (0) absent; (1) present. [new character].
- 159[135]. Female, metasoma, ovipositor sheath, transversal striations on basal half: (0) absent; (1) present. [modified from Quicke *et al.* 2009: char.107].
- 160[136]. Female, metasoma, ovipositor, length, relative to the apical width of metasoma: (0) less than; (1) distinctly longer than (Fig.14C). [modified from Gauld 1980: char.54; Gauld 1985: char.34; Quicke *et al.* 2009: char.113].
- 161[137]. Female, metasoma, ovipositor, angle relative to longitudinal metasomal axis, with ovipositor resting on its sheaths: (0) more than 90°; (1) less than 90°. [new character].
- 162[138]. Female, metasoma, ovipositor, shape, in lateral view: (0) virtually straight (Fig.14B); (1) curved upwards (Fig.14C); (2) curved downwards. [new character].
- 163[139]. Female, metasoma, ovipositor, apical half of dorsal valve, pre-apical notch: (0) absent; (1) present (Fig.14B). [modified from Quicke *et al.* 2009: char.112].

## Phylogenetic analysis

After coding all terminals (Appendix 1) a matrix was built (Appendix 2) including the 125 terminal taxa (114 for the ingroup and 11 for the outgroup) with 164 characters. The analysis resulted in eight equally parsimonious trees (L=1450.180), for which a strict consensus tree was generated (Figs 17–18).



**Figure 17.** Strict consensus of the eight most parsimonious trees found by the New technology search algorithms (Sec. search + Ratchet + Drift +Tree Fusing) on TNT software. Numbers on branches are Bremer support values. The black arrow points the beginning of the clade Ophioninae. “A” continued on Fig.18.



The subfamily Ophioninae (as recognized prior to this study, including all 32 genera) was recovered as clade (Figs 17–18) supported by seven discrete synapomorphies (Fig.19), two of which are uniquely derived: Hind legs with pectinae sinuous, occurring also on internal and/or external surfaces of claw (Char. 116[92]); and the forewing vein 2rs-m (1) opposite to, or (2) distad of 2m-cu vein (Char. 130[106]).

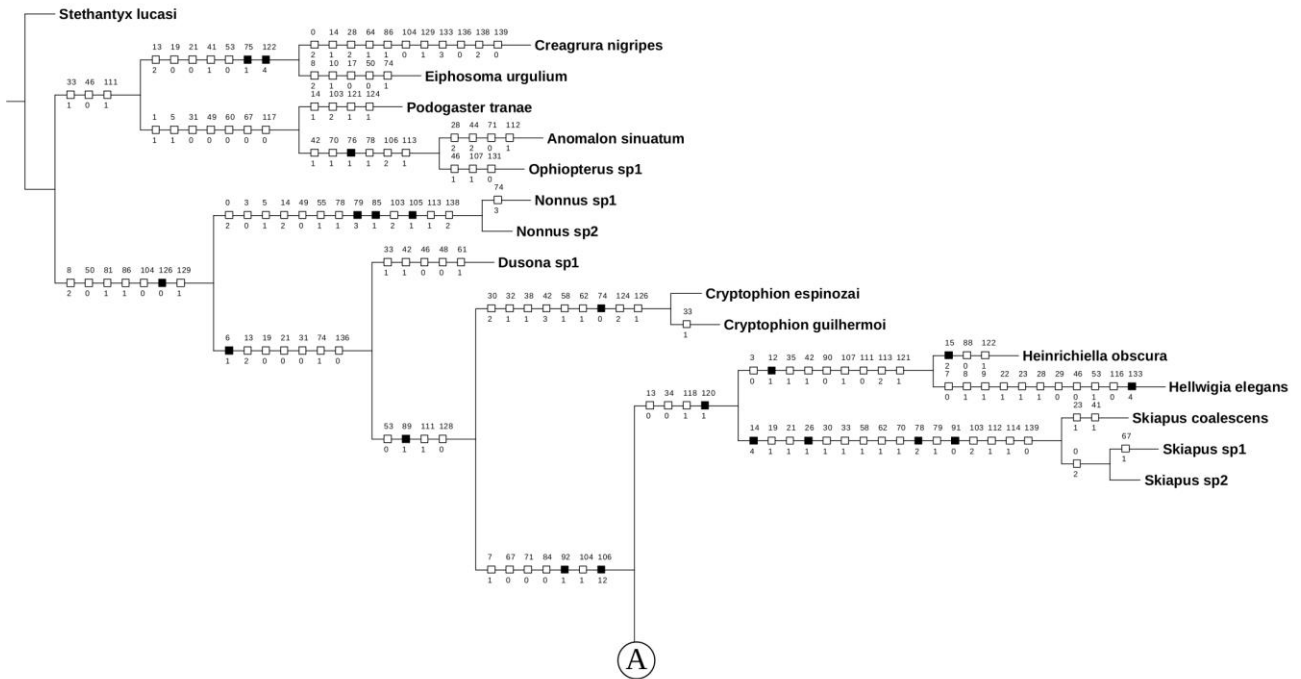
The clade ((*Heinrichiella* + *Hellwigia*) *Skiapus*) is supported by four synapomorphies, one of which is uniquely derived (Fig.19): Hindwing distal hamuli (on vein R1) with (1) first hamulus close to base of R1 by at least same distance to the second hamulus (Char. 144[120]). This clade is sister group to all other Ophioninae in the analysis. This is the first phylogeny to corroborates the proposition of a clade '*Hellwigia*' + *Skiapus* as basal divergence in Ophioninae (Quicke *et al.* 2005; Rouse *et al.* 2016). In a very recent research, Shaw and Voogd (2019) proposed the revalidation of *Heinrichiella*, changing to it a species from *Hellwigia*, making both genera monotypic. In the present analysis were found nine synapomorphies to the couple *Heinrichiella* + *Hellwigia*, one of which is uniquely derived: Dorsal edge of mandible with (1) sharp tooth-like lamella (Char. 36[12]).

Gauld (1985) proposed the Palearctic genus *Barytatocephalus* as part of *Thyreodon* genus-group (*Thyreodon* + *Barytatocephalus* + *Euryophion* + *Rhynchophion* + *Dictyonotus*), based on morphology, which was not supported by molecular analysis of Rouse *et al.* (2016). Here *Barytatocephalus mocsaryi* was recovered as sister group to the remainder Ophioninae (Fig.19), which is supported by six synapomorphies, two of

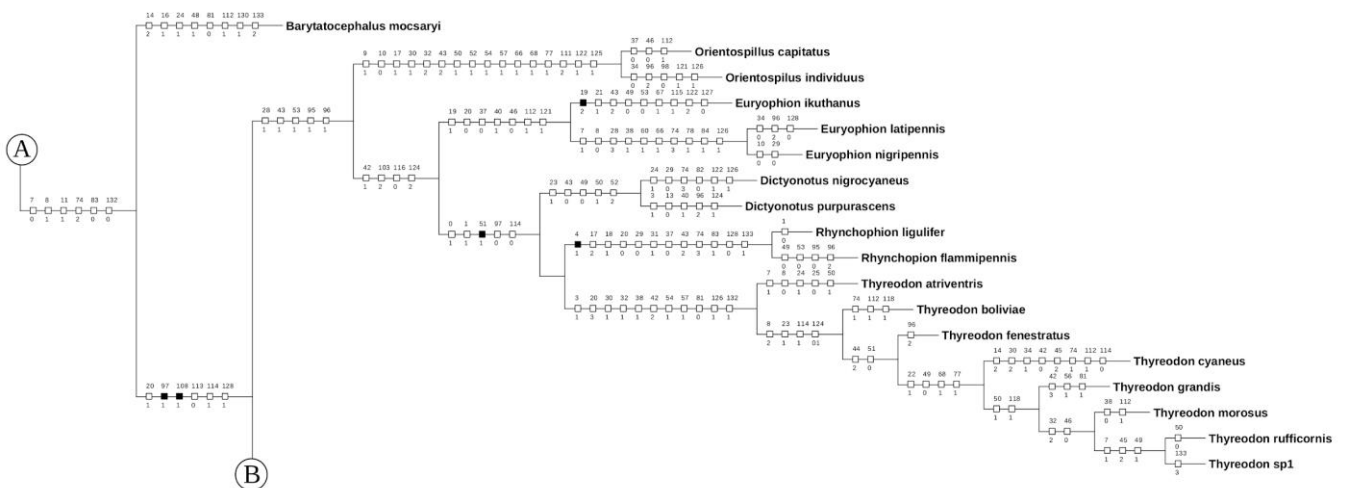
which are uniquely derived: forewing discosubmarginal cell anterior glabrous area (at least near pterostigma, but possibly along the Rs+2r vein) (1) present (Char. 121[97]); forewing spurious vein (on second subdiscal cell) paralleling wing margin (1) present (Char. 132[108]).

The clade comprising *Orientospilus*, *Euryophion*, *Dictyonotus*, *Rhynchophion* and *Thyreodon* is supported by five synapomorphies (Fig.20). This composition is similar to the *Thyreodon* genus-group of Gauld (1985) with the exclusion *Barytatocephalus* and inclusion of *Orientospilus*. Except for some *Thyreodon*, this group is represented by apparently diurnal Ophioninae. Inside the clade, the small genus *Orientospilus* (Afrotropical and Oriental) is sister group to the clade supported by four synapomorphies (Fig.20). While *Orientospilus* is characterized by regular sized specimens (for Ichneumonidae patterns), its sister clade include some of the larger and more robust specimens in the subfamily. Inside the large sized body clade, *Euryophion* (Afrotropical) is sister group to Thyreodonini *sensu* Rouse *et al.* (2016), which is supported by five synapomorphies, one of which is uniquely derived: hind margin of metanotum (1) swollen backwards, directed to propodeal spiracle (Char. 75[51]). The genus *Dictyonotus* (Afrotropical, Palearctic and Oriental) is sister group to the New World Clade (Nearctic + Panamanian + Neotropic) including *Rhynchophion* and *Thyreodon*.





**Figure 19.** Strict consensus shown in Fig.17 with the WINCLADA optimization of discrete characters, using unambiguous scheme. Numbers above boxes are character numbers as presented inside square brackets on character list and on heading of discrete matrix (Appendix 2). Numbers below boxes are character states. Black boxes represent uniquely derived character states. White boxes represent homoplastic derived character states. “A” continued on Fig.20.



**Figure 20.** Strict consensus continued from Fig.19. “B” continued on Fig.21.

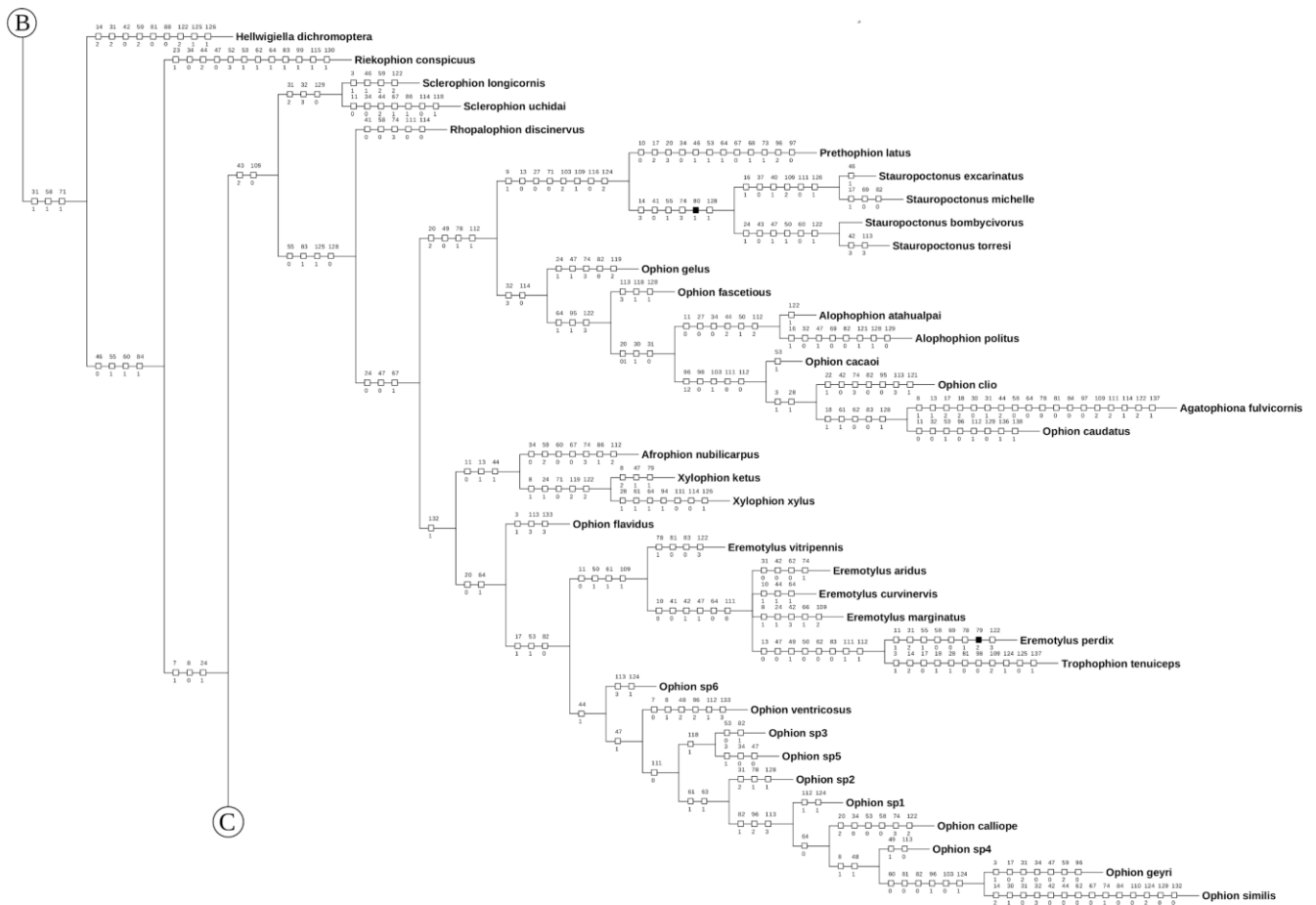
The genus *Hellwigiella* (Palearctic, Saharo-Arabian) is sister group to the remainder Ophioninae (Fig.21). This position is highly supported by the continuous characters and some aberrant discrete characters further discussed by Lima (2018) (Annex II).

With the exception of *Prethophion*, *Stauropoctonus*, *Eremotylus* and *Trophophion*, the relationship of *Sclerophion*, *Rhopalophion*, *Ophion*, *Alophophion*, *Agatophiona*, *Afrophion* and *Xylophion* was already proposed by Gauld (1985), in his *Ophion* genus-group. Coincidentally, two discrete synapomorphies (Fig.21) supporting the clade here were also proposed as synapomorphies by Gauld (1985): Posterior transverse carina of mesosternum (= pospectal) restricted to lateral vestiges. (Char. 67[43] = 2); and forewing vein 1m-cu angled (Char. 133[109] = 0).

Gauld (1985) supposed that all genera in his *Ophion* genus group could have arisen from a stem-group *Ophion*, while Schwarzfeld *et al.* (2016) using molecular data recovered the *Ophion* as a clade, independent from the other close genera included in the analysis (the same genera analysed by Gauld 1985). Although reconsidered in several studies (Gauld 1980, 1985; Schwarzfeld & Sperling 2014, 2015; Schwarzfeld *et al.* 2016), there is no consensus about *Ophion*, except that its diversity is still grossly underestimated, with many cryptic species hardly differentiated by morphology. Defining *Ophion* (and some related genera) is a task far beyond the resolution of the present analysis. Nonetheless, some internal relationship in this clade are highly supported here and allow some propositions. The present analysis corroborates some of the suppositions

made by Gauld (1985) recovering *Ophion* including *Alophophon*, *Agatophiona*, *Afrophion*, *Xylophion*, *Prethophon*, *Stauropoctonus*, *Eremotylus* and *Trophophon*. The genera *Sclerophon* and *Rhopalophon* diverge before *Ophion*, which could be a result of an insufficient *Ophion* sampling. The monotypic genus *Agatophiona* (Nearctic) is well supported as a derived species inside *Ophion*, sister of *Ophion caudatus* (Oriental) (Fig.21), a highly differentiated *Ophion* species, with long curved ovipositor and with specialized labiomaxillary complex. The five species included of *Eremotylus* (Palearctic, Nearctic, Neotropical, Saharo-Arabian and Sino-Japanese) were recovered in a polytomy with the monotypic genus *Trophophon* (Nearctic) (Fig.17). Although there is no support (Bremer) for the internal relationship, the discrete characters alone suggest that *Trophophon* may be a derived species of *Eremotylus* (Fig.21).

The remainder Ophioninae, most of which were originally included in the *Enicospilus* genus-group (Gauld 1985) are divided into two clades (Fig. 22). The first clade includes *Janzophon*, *Pamophon*, *Laticoleus*, *Lepiscelus*, *Simophon*, *Ophiogastrella* and *Leptophon*. All genera were recovered monophyletic, except for *Laticoleus* (Afrotropical) which is paraphyletic for a clade comprising *Lepiscelus*, *Simophon*, *Ophiogastrella* and *Leptophon* (Fig. 22). This paraphyly is assumed to be a result of bad sampling, as for three of the four species included (*Laticoleus infumatus*, *L. longicornis* and *L. palpalis*) only one specimen was analysed, all missing the metasomal apex.



**Figure 21.** Strict consensus continued from Fig.20. “C” continued on Fig. 22

The other clade includes *Riekophion* (part), *Dicamptus*, *Sicophion* and *Enicospilus* (Fig. 22). Most of these genera were already recovered closely related (Gauld 1985; Rouse *et al.* 2016). Nonetheless, this is the first time *Enicospilus* is recovered paraphyletic with respect to *Sicophion*, a small genus with only three described species, one Panamanian and two Neotropical, all characterized by the specialization of the labiomaxillary complex, elongation of legs and forewing vein Rs centrally dipped.

The small genus *Riekophion* have only three species, all restricted to Australian region. The morphological definition of this genus is consistent and well described by Gauld (1977). The position of *R. conspicuus* in the

present analysis (Fig.21) is supposed to be an artefact of the absence of females for coding the characters. It is assumed here that the genus would stay close to the *Enicospilus* lineage, as the position of *Riekophion emandibulator* (Fig. 22).

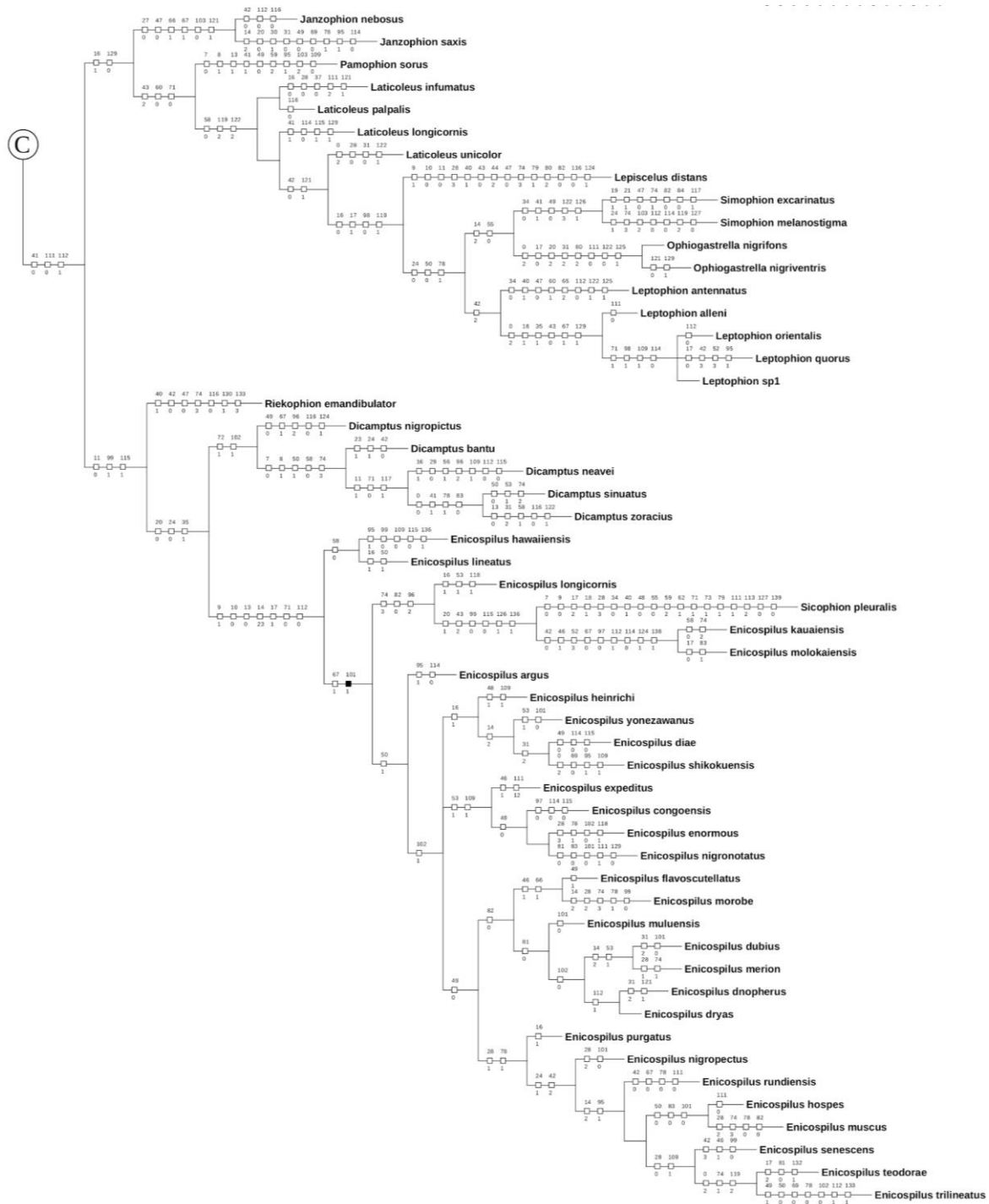


Figure 22. Strict consensus continued from Fig.21.

## Remarks on selected characters

Some of the characters used here deserve highlighting for their traditional or potential use in the taxonomy of Ophioninae (and Ichneumonidae) and for their (potential) biological significance.

The *ophionoid facies*, whose relative large ocelli are a main component, have always been used as a reference for the Ophioninae. The present analysis included two continuous characters related to the relative size of ocelli, characters 1 and 2. Although both characters are related to the ocelli size (the larger the ocelli, the higher the value of char.1 and the lower the value of char.2), the large amount of measured specimens support that there is independence in the information contained in both characters, justifying the use of both (Fig. 23). The phylogeny reconstructed here supports the large increase in ocellus size (Char.1  $\geq 0.17$ ; Char.2  $< 0.2$ ) occurring in the ancestral lineage of Enicospilini + Ophionini, and independently in *Euryophion* and in some *Thyreodon* species, with few reversals (Figs 23–24). Knowing that the relatively large sized ocelli is a morphological adaptation correlated with nocturnal habits, it can be assumed that the nocturnal habits is not present on the origin of the subfamily, it is a derived character inside Ophioninae clade.



(Cushman 1947), due to the LmCS and long curved ovipositor. In the description of *S. pleuralis* there is the statement ‘maxillae somewhat elongated’ (Gauld 1980), but clearly both glossa and galeae are elongated (maxilla and labium respectively). The figures presented by Cushman (1947) suggest differences in the LmCS from *O. caudatus* and *T. tenuiceps*. Sadly it was not possible to verify in further detail the morphology of the specimens available (old and damaged specimens) to propose different states.

The pilosity on ventral surface of hind leg, its absence (Char105[81]) and curvature (Char106[82]) are new proposed characters. They are here supposed to be a result of the position of legs during the pupal stage (due to the contact of femur and tibia) as it was not possible to identify scars from fallen setae or any other sign that could suggest the setae fallen during the adult life. Inside Ophioninae, the absence of such setae is synapomorphic for *Thyreodon*, *Hellwigiella*, *Agathophiona* and *Trophophion*, and also observed in *Ophion* and *Eremotylus* species (Fig. 26).

The coding of intercubital veins among Ichneumonidae is a very controversial question. Historically, when the areolet is open, the single intercubital vein is called either 2rs-m (= 2rm or 2Rs) or 3rs-m (=3rm) according to its position related to vein 2m-cu (Broad *et al.* 2018; Bennett *et al.* 2019; Wahl 1991) or it can be even called 2+3rm, when interpreted as the fusion of both intercubital veins (Gauld 1976). It is impossible to say at this time whether the only intercubital vein in Ichneumonidae is the result of loss, fusion or both processes. Nonetheless, naming the vein according to its position means to assume that in two specimens with the single intercubital



vein differentially placed (relative to 2m-cu) these veins are not homologous. The coding proposed here (Char.128[104]) considers that the single intercubital vein (in the seen Ichneumonidae) is the 2rs-m. This proposition is based on two observations: (1) In all seen Ichneumonidae with a closed areolet, the 3rs-m (second intercubital) possesses a bulla, closer to M than to Rs. When areolet is open, the single intercubital vein has no bulla; (2) the position of the single intercubital vein is quite variable in some groups, such as Anomaloninae, with extreme cases such as *Habronyx heros*, with specimens presenting the intercubital vein basad, opposite or distad of 2m-cu (Gauld 1976).

Gauld (1985) proposed the possession of a spurious vein on second subdiscal cell paralleling wing margin (132[108]) as a synapomorphy of Ophioninae. Present analysis recovered such character not as synapomorphy for the entire Ophioninae (Fig. 27), but for an internal clade, excluding *Hellwigia*, *Heinrichiella*, *Skiapus* and *Barytatocephalus*, although in Rousse *et al.* (2016) *B. mocsaryi* was coded with this vein present.

The loss of basal hamuli (Char.140[116]) is for the first time recovered as a synapomorphy for the clades (*Euryophion* + (*Dictyonotus* + (*Rhynchophion* + *Thyreodon*))) and (*Prethophion* + *Stauropogon*), besides an autapomorphic appearance in *Hellwigia*, *Lepiscelus*, and species of *Janzophion*, *Laticoleus*, *Riekophion* and *Dicamptus* (Fig. 28). The presence of the hamuli is a key character for the Hymenoptera, and their loss or reduction could harm their wasps' ability to fly. In the Ophioninae lineage this problem was solved by an

increase in the number of distal hamuli (relative to the mean) in all terminals except *Lepiscelus* and neotropical species of *Stauropogon*.

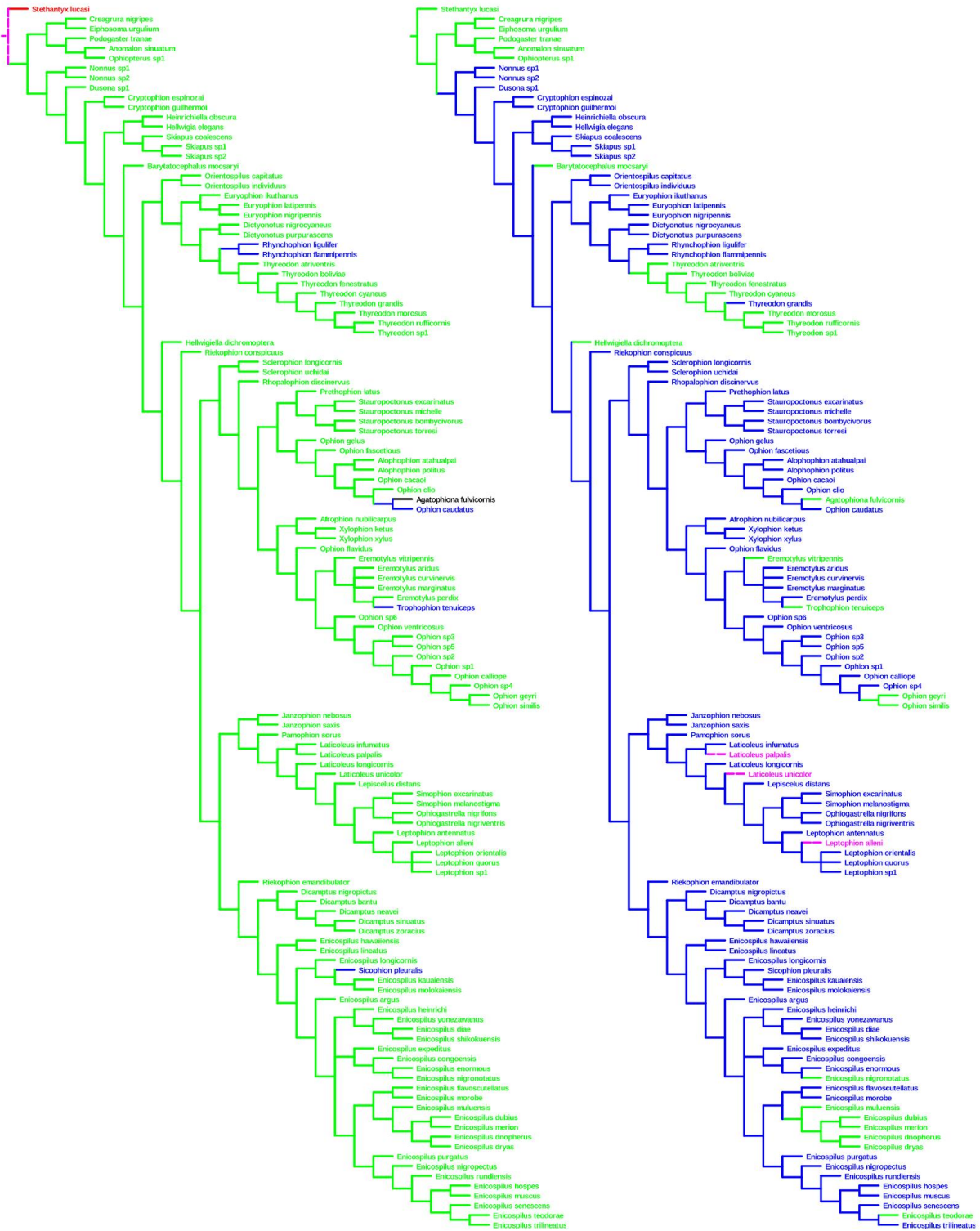
Ophioninae species are known to have a very short ovipositor, which is consistent with known biological data that they are koinobiont endoparasitoids attacking exposed Lepidoptera larvae. Thus the long ovipositor (Char.160[136]) found in *O. caudatus*, *E. hawaiiensis* and *E. kauaiensis* (Fig. 14) signals for an adaptive shift to attack concealed larvae. The long ovipositor in Ophioninae is only known in *Enicospilus* from Hawaii, *E. terebrus* (New Guinea) and *O. caudatus* (Oriental) (Fig. 28).

The possession of a sinuous pectinal comb on the tarsal claws was proposed by Gauld (1985) as a synapomorphy for Ophioninae. Since then, all posterior phylogenies have used at least one character in this way, agreeing with Gauld's proposition. After observation of all specimens used here, the need for more sophisticated coding for this feature became clear: there is an intraspecific variation related to (1) the sex of the specimen, with different types of pectinae for each sex; and to (2) which leg is observed (fore and midleg tarsal claws are almost equal, while hindleg may be either similar or completely different). In order to deal with this variation, this complex feature was coded in eight characters (Chars 111[87] to 118[94]). Not surprisingly, as proposed by Gauld (1985), the sinuous pectinal comb was recovered as a synapomorphy for subfamily, but for the first time including *Hellwigia*, *Heinrichiella* and *Skiapus*. These three genera have the pectinal comb very reduced when compared with remainder Ophioninae. The closely related *Hellwigia* and *Heinrichiella* have pectinae absent on hind legs, and

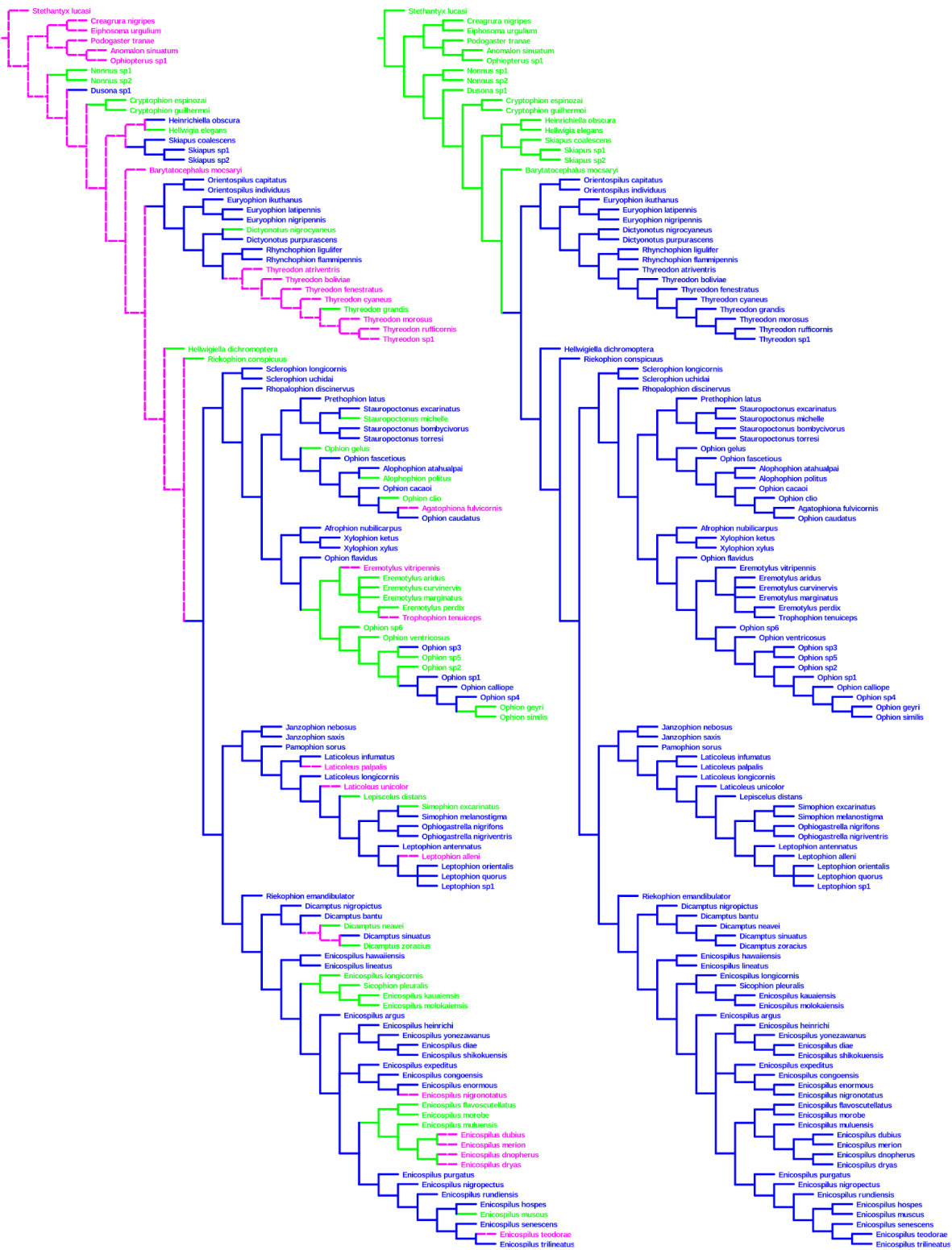




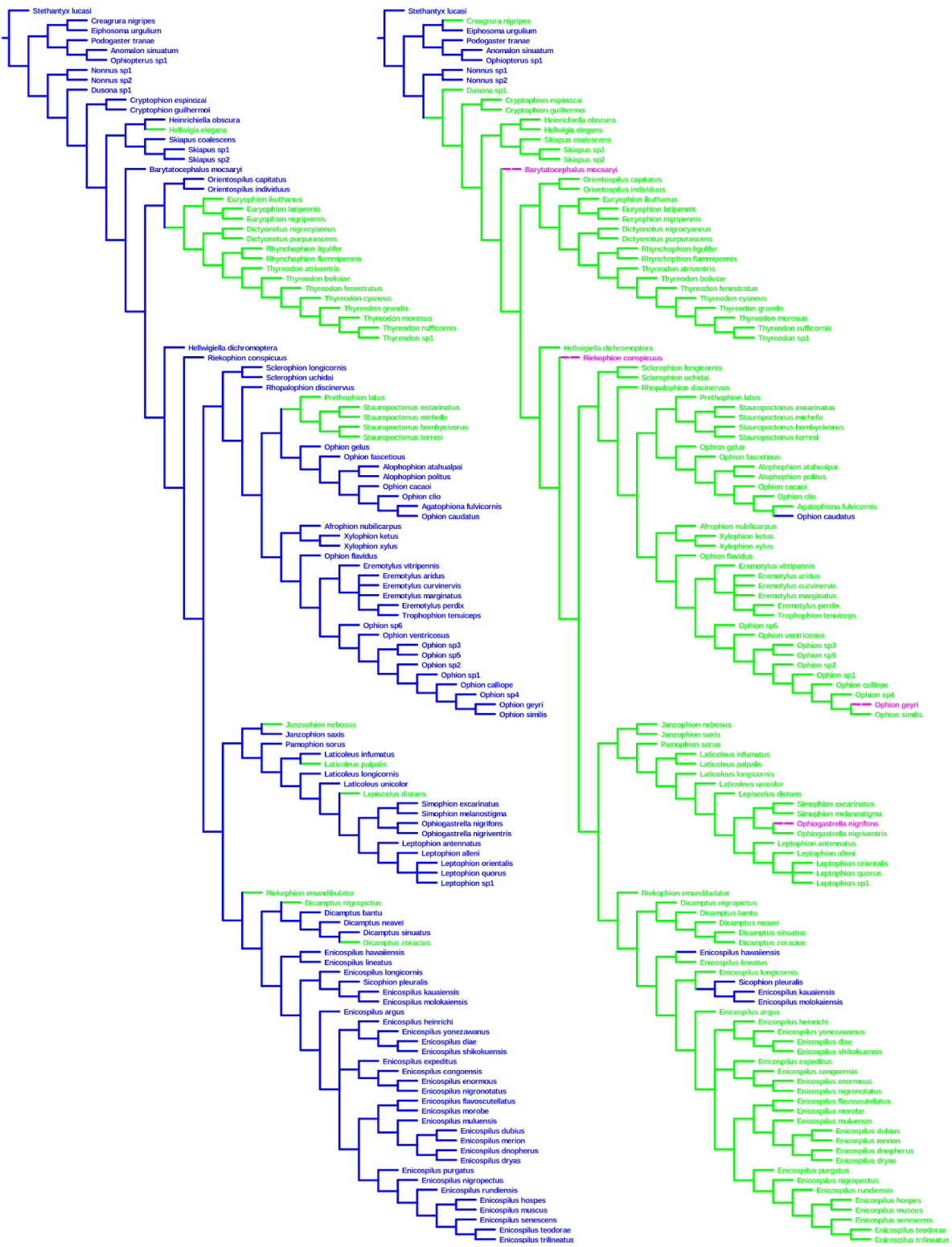
**Figure 25.** Character mapping on strict consensus tree, using TNT software: Char.2. Numbers on branches are the Log10(x+1) value of ratio of posterior ocellus distance from eye / ocellar maximum length.



**Figure 26.** Character mapping on strict consensus tree, using WINCLADA software: (left) Char.42[18], labiomaxillary complex specialization; and (right) Char.105[81], presence of hind femur ventral pilosity. Colours represent states as follow: green (0); blue (1); black (2); red (3); yellow (4); and pink (ambiguity).



**Figure 27.** Character mapping on strict consensus tree, using WINCLADA software: (left) Char.106[82], presence of backward curved pilosity on hind femur ventral surface; and (right) Char.132[108], presence of forewing spurious vein. Colours represent states as follow: green (0); blue (1); and pink (ambiguity).



**Figure 28.** Character mapping on strict consensus tree, using WINCLADA software: (left) Char.140[116], presence hindwing basal hamuli; and (right) Char.160[136], relative length of female ovipositor. Colours represent states as follow: green (0); blue (1); and pink (ambiguity).

## **Taxonomy**

Traditionally in Ophioninae classification it is common the use of ‘genus-group’ and ‘species-group’ rather than formal taxonomy categories. They are specially useful when there is no cladistic support for the groups, but quite often these sometimes giant expressions lead to misunderstandings, undermining one of the main purposes of classifications, which is to be useful for communication. Since cladistic support for groups exists, formal taxonomic categories are perfectly accepted. According to these ideas and the results discussed above, a new classification is proposed for Ophioninae.

### **OPHIONINAE** Shuckard, 1840

#### **HELLWIGIINI** Förster, 1869 **stat. rev.**

Type genus: *Hellwigia* Gravenhorst, 1823.

Diagnosis: Ocelli small; antennae at most as long as forewing, usually shorter; mandible without basal swelling; epicnemial carina present on mesopleuron; sternaulus absent; posterior transverse carina (= postpectal) complete; notaulices vestigial or indistinct; scutellar carinae present for more than  $\frac{2}{3}$  the scutellum length; fore tibia without membranous flange behind macrotrichial comb of tibial spur; hind femur ventrally with pilosity on median line; hind tibia without comb of dense setae on posterior margin; forewing hyaline; vein Rs+2r centrally straight; without spurious vein on second subdiscal cell; vein 1m-cu more or less curved, without sharp angle; discosubmarginal cell without anterior glabrous area; hindwing usually with basal hamuli present; distal hamuli on vein R1 clearly forming a proximal



grouping, with basalmost hamulus closer to base of R1 vein than to the nearest hamulus; metasomal tergite II without umbo, with laterotergite folded beneath tergite; female with a crease at least partly separating metasomal tergite II from laterotergite; ovipositor virtually straight, shorter than apical width of metasoma.

Included genera: *Heinrichiella* Hedwig, 1949, *Hellwigia* Gravenhorst, 1823 and *Skiapus* Morley, 1917.

Distribution: Afrotropical, Palearctic and Saharo-Arabian.

Comments: Hellwigiini is here revalidated as proposed by Townes (1969). Both *Heinrichiella* and *Hellwigia* are monotypic. *Skiapus* has three described and at least four undescribed species, which are included in an ongoing genus review co-authored by the author of this thesis. All genera in this tribe have tarsal pectinal comb reduced, with the extreme *Heinrichiella* and *Hellwigia*, in which the hind tarsal claws are simple.

#### THYREODONINI Rouse *et al.*, 2016

Type genus: *Thyreodon* Brullé, 1846.

Diagnosis: Ocelli generally small; antennae at most as long as forewing, usually shorter; mandible with basal swelling; epicnemial carina either present or absent on mesopleuron; sternaulus present or absent; posterior transverse carina (= pospectal) from complete to restricted to lateral vestiges; notaulices vestigial or sharply impressed and reaching beyond centre of mesoscutum; scutellar carinae absent or present, from restricted to basal third to extended for more than  $\frac{2}{3}$  the scutellum length; fore tibia without

membranous flange behind macrotrichial comb of tibial spur; hind femur ventrally with or without pilosity on median line; hind tibia usually without comb of dense setae on posterior margin; forewing hyaline, dark infusate or with a golden reflex with small infuscated areas; vein Rs+2r centrally straight; with spurious vein on second subdiscal cell paralleling wing margin; vein 1m-cu more or less curved, without sharp angle; discosubmarginal cell with anterior glabrous area absent or present, along the thickest portion Rs+2r vein, without sclerites; hindwing usually without basal hamuli; distal hamuli on vein R1 either equally interspaced or forming a clear proximal grouping, always with basalmost hamulus closer to the nearest hamulus than to base of R1 vein; metasomal tergite II usually without umbo (except *Orientospilus*), with laterotergite either folded beneath tergite or pendant; female without crease on metasomal tergite II; ovipositor virtually straight, shorter than apical width of metasoma.

Included genera: *Dictyonotus* Kriechbaumer, 1894, *Euryophion* Cameron, 1906, *Orientospilus* Morley, 1912, *Rhynchophion* Enderlein, 1912 and *Thyreodon* Brullé, 1846.

Distribution: Afrotropical, Madagascan, Nearctic, Neotropical, Oriental, Palearctic, Panamanian and Sino-Japanese.

Comments: The tribe proposed by Rouse *et al.* (2016) is reconsidered to include and *Euryophion* and *Orientospilus*.

#### **OPHIONINI** Shuckard, 1840

Type genus: *Ophion* Fabricius, 1798.

Diagnosis: Ocelli large, rarely small; antennae longer than forewing; mandible with or without basal swelling; epicnemial carina usually present on mesopleuron, rarely absent; sternaulus absent; posterior transverse carina (= pospectal) restricted to lateral vestiges, rarely more complete; notaulices from vestigial to sharply impressed and reaching beyond centre of mesoscutum; scutellar carinae absent or present, from restricted to basal third to extended for more than  $\frac{2}{3}$  the scutellum length; fore tibia with or without membranous flange behind macrotrichial comb of tibial spur; hind femur usually with ventral pilosity on median line; hind tibia usually with comb of dense setae on posterior margin; forewing hyaline, dark infusate or with a golden reflex with small infuscated areas; vein Rs+2r centrally straight; with spurious vein on second subdiscal cell paralleling wing margin; vein 1m-cu usually angled and with ramellus, less frequent sinuous or more or less curved, without ramellus; discosubmarginal cell with anterior glabrous area absent or present, along the thickest portion Rs+2r vein, without sclerites; hindwing usually with basal hamuli present; distal hamuli on vein R1 usually equally interspace or rarely forming a proximal grouping, always with basalmost hamulus closer to the nearest hamulus than to base of R1 vein; metasomal tergite II usually with umbo, with laterotergite folded beneath tergite; female without crease on metasomal tergite II; ovipositor usually straight and shorter than apical width of metasoma.

Included genera: *Afrophion* Gauld, 1979, *Alophophion* Cushman, 1947, *Eremotylus* Förster, 1869, *Ophion* Fabricius, 1798 [*Agathophiona* Westwood, 1882 **syn. n.**], *Prethophion* Townes, 1971, *Rhopalophion* Seyrig, 1935,

*Sclerophion* Gauld, 1979, *Stauropoctonus* Brauns, 1889, *Trophophion* Cushman, 1947 and *Xylophion* Gauld, 1979.

Distribution: Afrotropical, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental, Palearctic, Panamanian, Saharo-Arabian and Sino-Japanese.

Comments: *Ophion* is not monophyletic, as discussed above, however the sampling was not enough to clearly define it, the same for the associated genera. Thus, in order not to disrupt classification with many changes not strongly supported, which in a near future can easily be changed with a better sampling, only one change is proposed, the synonymization of *Agathophiona* under *Ophion*.

#### **ENICOSPILINI** Townes, 1971

Type genus: *Enicospilus* Stephens, 1835.

Diagnosis: Ocelli large, rarely small; antennae longer than forewing; mandible with or without basal swelling; epicnemial carina usually present on mesopleuron, rarely absent; sternaulus absent; posterior transverse carina (= postpectal) complete or reduced to lateral vestiges; notaulices usually vestigial or indistinct, rarely sharply impressed and reaching beyond centre of mesoscutum; scutellar carinae absent or present, from restricted to basal third to extended for more than  $\frac{2}{3}$  the scutellum length; fore tibia with or without membranous flange behind macrotrichial comb of tibial spur; hind femur usually with ventral pilosity on median line, rarely without it; hind tibia usually with comb of dense setae on posterior margin; forewing

usually hyaline, rarely with golden reflex; vein Rs+2r centrally straight to sinuous; with spurious vein on second subdiscal cell paralleling wing margin; vein 1m-cu usually more or less curved, rarely with sharp angle with or without ramellus; discosubmarginal cell with or without anterior glabrous area, with or without sclerites; hindwing with basal hamuli present or absent; distal hamuli on vein R1 usually equally interspaced or rarely forming a proximal grouping, always with basalmost hamulus closer to the nearest hamulus than to base of R1 vein; metasomal tergite II usually without umbo and with laterotergite folded beneath tergite, rarely with umbo or laterotergite pendant; female without crease on metasomal tergite II; ovipositor usually straight and shorter than apical width of metasoma.

Included genera: *Dicamptus* Szépligeti, 1905, *Enicospilus* Stephens, 1835 [*Sicophion* Gauld, 1979 **syn. n.**], *Janzophion* Gauld, 1985, *Laticoleus* Townes, 1973, *Lepiscelus* Townes, 1971, *Leptophion* Cameron, 1901, *Ophiogastrella* Brues, 1912, *Pamophion* Gauld, 1977, *Riekophion* Gauld, 1977 and *Simophion* Cushman, 1947.

Distribution: Afrotropical, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental, Palearctic, Panamanian, Saharo-Arabian and Sino-Japanese.

Comments: In the analysis both *Laticoleus* and *Riekophion* were recovered non monophyletic, which is supposed to be the result of bad sampling and lack of females, respectively. Thus the only change proposed here is the synonymization of *Sicophion* under *Enicospilus*. This change will require

another change, as *Sicophion fenestralis* Gauld, 1988 will be considered junior homonym of *Enicospilus fenestralis* (Szépligeti, 1906).

**BARYTATOCEPHALINI** Lima, 2019 **trib. n.**

Type genus: *Barytatocephalus* Schulz, 1911.

Diagnosis: Ocelli small; antennae slightly longer than forewing; mandible with basal swelling; epicnemial carina present on mesopleuron; sternaulus absent; posterior transverse carina (= pospectal) complete; notaulices vestigial or indistinct; scutellar carinae present for between  $\frac{1}{3}$  and  $\frac{2}{3}$  the scutellum length; fore tibia without membranous flange behind macrotrichial comb of tibial spur; hind femur ventrally without pilosity on median line; hind tibia without comb of dense setae on posterior margin; forewing hyaline; vein Rs+2r centrally straight; without spurious vein on second subdiscal cell; vein 1m-cu more or less curved, without sharp angle; discosubmarginal cell without anterior glabrous area; hindwing with basal hamuli present; distal hamuli on vein R1 equally interspaced, with basalmost hamulus closer to the nearest hamulus than to base of R1 vein; metasomal tergite II without umbo, with laterotergite folded beneath tergite; female without crease on metasomal tergite II; ovipositor virtually straight, shorter than apical width of metasoma.

Included genus: *Barytatocephalus* Schulz, 1911.

Distribution: Palearctic.

**HELLWIGIELLINI** Lima, 2019 **trib. n.**

Type genus: *Hellwigiella* Szépligeti, 1905.

Diagnosis: Ocelli small; antennae slightly longer than forewing; mandible with basal swelling; epicnemial carina present on mesopleuron; sternaulus absent; posterior transverse carina (= pospectal) complete; notaulices vestigial or indistinct; scutellar carinae present for more than  $\frac{2}{3}$  the scutellum length; fore tibia with a membranous flange behind macrotrichial comb of tibial spur; hind femur ventrally without pilosity on median line; hind tibia without comb of dense setae on posterior margin; forewing hyaline; vein Rs+2r centrally straight; with spurious vein on second subdiscal cell paralleling wing margin; vein 1m-cu more or less curved, without sharp angle; discosubmarginal cell with anterior glabrous area along the thickest portion Rs+2r vein, without sclerites; hindwing with basal hamuli present; distal hamuli on vein R1 equally interspaced, with basalmost hamulus closer to the nearest hamulus than to base of R1 vein; metasomal tergite II with umbo, with laterotergite folded beneath tergite; female without crease on metasomal tergite II; ovipositor virtually straight, shorter than apical width of metasoma.

Included genus: *Hellwigiella* Szépligeti, 1905.

Distribution: Palearctic and Saharo-Arabian.

Comments: The unusual morphology and distribution of the single genus in this tribe was recently revised (Lima 2018).

## Concluding Remarks

This is the most complete cladistic analysis of Ophioninae performed so far, sampling species from all valid genera. Previous used characters were evaluated and new ones proposed, using a clear definition of states. Pioneering, continuous characters were employed in ophionine cladistics, and for first time the subfamily have morphological support for monophyly including all valid genera.

A complete suprageneric classification for Ophioninae is proposed using formal taxonomic categories, with changes on tribes Enicospilini, Ophionini and Thyreodonini, revalidation of Hellwigiini, and proposition of Barytatocephalini and Hellwigiellini as new tribes.

Among the previous valid genera, only *Laticoleus*, *Riekophion*, *Ophion* and *Enicospilus* were not revered monophyletic. Taking into account the sampling limitations to define *Ophion* and the particularities about *Riekophion* and *Laticoleus*, only two synonymizations were proposed, *Agathophiona* under *Ophion* and *Sicophion* under *Enicospilus*.

The present cladistic analysis improves the understanding of Ophioninae and internal generic relationships, supporting improvements in classification and offering good morphological recognisable characters to support clades.



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## Appendix 1

Specimens employed in the morphological cladistic analysis of the Ophioninae. Locations are listed in alphabetical order with countries and Brazilian states in bold. Type specimens are marked in bold. The question mark '?' within parentheses, after the species name, means specimens with unidentifiable sex, due the lack of metasoma apex. The question mark '?' aside of a word means that information on specimen label was not fully readable. The information in square brackets was not present on the label but was deduced.

### EXAMINED SPECIMENS

#### INGROUP: OPHIONINAE:

1. *Afrophion nubilicarpus* (Tosquinet, 1896) (3♀) **Republic of South Africa**, Western Cape Cerderberge, Jamaka Farm, 32°20'S 19°01'E, 7–18.ix.2008, F. Koch *leg.* [ZMHB]; E. Cape Town Prov. Katberg. 4000 ft (Brit.Mus.1932-577) 14–26.xi.1932. R.E.Turner *leg.* [BMNH]; Jonkershoek near Stellenbosch 14.x.[19]70. V. Whitehead *leg.* [BMNH].
2. *Agathophiona fulvicornis* Westwood, 1882 (1♀, 1♂) **Mexico**, Guanajuato, A.Duges *leg.* [♂, SMNH, NHRS-HEVA6038]; Chapultepec. 1871, Bilimek *leg.* [♀, BMNH, P. Cameron coll. 1914-110].
3. *Alophophion atahualpai* Alvarado, 2014 (5♀, 1♂) **Peru**, Amazonas, Chachapoyas, 2800m 26.iii.1684, M. Cooper *leg.* {M. Cooper BMNH(E)2005-152} [♂, **PARATYPE**, BMNH]; CA., S.N., Udimá, Monteseco, 6°50'40.4"S; 79°03'45.53"W 3116m, 14–15.v.2010, J.Grados *leg.* [5♀, **PARATYPES**, BMNH].
4. *Alophophion politus* (Morley, 1912) (6♀, 3♂) **Chile**, Chubut, 18.vi.1962, A.Kovacs *leg.* B.M.1964-193 [2♀, BMNH]; Concepción, 21.xii.1905 P. Herbst {The label has a impressed date (1903), but there is a correction by hand over it, with 21.xii.1905} [♀, BMNH]; Maipo, Valley, 5.xi.1971, B.M.1973-192 [♀, BMNH]; Trata Victoria, 24.iii.1961, A.Kovacs *leg.*, B.M.1964-193 [♀, BMNH]; R.N. El Bolson, 30.x.1961, A.Kovacs *leg.*, B.M.1964-193 [♀, 3♂, BMNH].
5. *Barytatocephalus mocsaryi* (Brauns, 1895) (2♂) **Hungary**, Budap[est], Mocsáry[?] *leg.* [**LECTOTYPE**, ZMHB]; **Turkey**, Edirne, 6.v.1960, 50', Guichard & Harvey *leg.* B.M.1960-364 [BMNH].
6. *Dicamptus bantu* Delobel, 1976 (1♀, 1♂) **Democratic Republic of Congo**, Zaire, 8 Mi. W. of Luanza, 1330m, 15.i.1958, E. S. Ross & R. E. Leech *leg.* [♂, CAS]; Zaire, 19 Mi. W. of Kolwezi, 1370m, 9.i.1958, E. S. Ross & R. E. Leech *leg.* [♀, CAS].

7. *Dicamptus neavei* Gauld & Mitchell, 1978 (1♀) **Republic of South Africa**, N'dumu Game Reserve, 26°55'S, 32°19'E, 19.xi.1999, F. Koch leg. [ZMHB].
8. *Dicamptus nigropictus* (Matsumura, 1912) (1♀, 1♂) **Japan**, Kyoto Pref., Miyadu City, Kamiseya, Seyakogen, N35.639, E135.183, 500m, 18–19.vii.2015, Shunpei Fujie leg., light trap [♀, LIBES]; **Malaysia**, Sarawak, Mt. Mulu, vi.[19]78, Eastop[?] leg. [♂, BMNH].
9. *Dicamptus sinuatus* (Morley, 1913) (1♀, 1♂) No data [♂, BMNH]; **Sri Lanka**, no further data [♀, LECTOTYPE, BMNH].
10. *Dicamptus zoracius* Gauld & Mitchell, 1981 (1♀) **India**, locality data not legible [original description: Uttar Pradesh, Dehra Dun, x.31] T. R. Bell[?] leg. B.M. 1934-394 [HOLOTYPE, BMNH].
11. *Dictyonotus nigrocyaneus* (Tosquinet, 1903) (2♀, 1♂) **Republic of South Africa**, Pr Natal [♂, HOLOTYPE of *D. superbus*, B.M.TYPE HYM.3G1196, BMNH]; **Tanzania**, D.O.Afrika, Morogoro, 2–18.v.[19]26 Brandes S. G. leg. [♀, ZMHB]; **Zimbabwe**, Brit. S. Afr. Buluwayo, xii.1903, G. A. K. Marshal leg. 1907-52 [♀, HOLOTYPE of *D. magnificus*, B.M.TYPE HYM.3G1195, BMNH].
12. *Dictyonotus purpurascens* (Smith, 1874) (6♀) **China**, Tsingtau, Glaue S. leg. [ZMHB]; **Indonesia**, Sumatra, Soekaranda, i.1894, Dohrn leg. Mus. Zool. Polonicum Warszawa 12/45 [HOLOTYPE of *D. sumatranus*, MIIZ]; **Japan**, no further data [HOLOTYPE, B.M.TYPE HYM.3G1203, BMNH]; *idem*, 21.vii.2012 [LIBES]; **Korea**, no further data [HOLOTYPE of *D. metallicus*, ZMHB]; **Laos**, Sedone Prov., Pakse, 30.vi.1967, Native collector [BM].
13. *Enicospilus argus* Gauld & Mitchell, 1981 (1♂) **New Guinea**, NE Wau, 1200m, 30.xii.1964, J.L.Gressitt leg. [PARATYPE, BM].
14. *Enicospilus congoensis* (Cameron, 1912) (1♀) **S.R.A.**, Hluhluwe Game Reserve, 28°02'S; 32°05"E, 5.xii.1995, F.Koch leg. [ZMHB].
15. *Enicospilus diae* Lima & Kumagai, 2012 (4♀, 3♂) **Brazil, Minas Gerais**, Belo Horizonte, Estação Ecológica - UFMG, 19°52'29.9"S; 43°58'20.3"W, 842m, 1.xii.2000, A.F.Kumagai leg., Malaise [♀, HOLOTYPE, UFMG-IHY-1700000, CCT-UFMG]; *idem*, 15.x.1998 [PARATYPES, ♀, UFMG-IHY-1700034, ♂, UFMG-IHY-1700061, CCT-UFMG], 21.x.1991 [PARATYPES, ♀, UFMG-IHY-1700035, ♂, UFMG-IHY-1700050, CCT-UFMG], 29.ix.2000 [♂, UFMG-IHY-1700063, PARATYPE, CCT-UFMG], 4.xii.1998 [♀, UFMG-IHY-1700037, PARATYPE, CCT-UFMG].
16. *Enicospilus dnopherus* Gauld & Mitchell, 1981 (1♀) **D.N.Guinea**, ?Bukuria, 18.iv.[19]09, Neuhauss L.G. leg. [PARATYPE, ZMHB].
17. *Enicospilus dryas* Gauld & Mitchell, 1981 (1♀) **New Guinea**, NE Mt. Kaindi 2400m 27.i.1963 J. Sedlacek leg. [PARATYPE, BM].
18. *Enicospilus dubius* (Tosquinet, 1896) (1♀) **Gana**, Bismarckburg, Togoland, R.Büttner S. leg. [LECTOTYPE, ZMHB].

19. *Enicospilus enormous* Gauld & Mitchell, 1981 (1♀, 1♂) **New Guinea**, NE Min Finisterre Range nr. Freyberg Pass (N), 2550m, 1–21.x.1958, W.W.Brandt leg. [♂, **PARATYPE**, BM]; (NE) Mt. Kaindi, 16km SW of Wau, 2300m 5–7.x.1962 J. Sedlacek leg., Light Trap [♀, **PARATYPE**, BM].
20. *Enicospilus expeditus* (Tosquinet, 1896) (1♀) **Togo**, Hinterland, West Afrika, Kling S. leg. [**HOLOTYPE**, ZMHB]
21. *Enicospilus flavoscutellatus* (Brullé, 1846) (3♀, 3♂) **Brazil, Minas Gerais**, Serra do Salitre, RPPN Cachoeira do Campo, 19°09'44.4"S; 46°34'08"W, 1043m, 13.x.2012, A.R.Lima & A.F.Kumagai leg. [♀, UFMG-IHY-1905430, CCT-UFMG]; *idem*, 11–15.x.2012 [♂, UFMG-IHY-1905433, CCT-UFMG]; **Paraná**, Curitiba, Bosque Capão da Imbuia, 26.xii.2002, A.F.Kumagai leg., Malaise [♀, UFMG-IHY-1905432, CCT-UFMG]; *idem*, 14.i.2003 [♂, UFMG-IHY-1905434, CCT-UFMG], 22.xii.1955 [♂, UFMG-IHY-1905434, CCT-UFMG]; **São Paulo**, Jundiaí, Serra do Japi, sobre vegetação, 19.v.1988, F.Friero-Costa leg. [♀, UFMG-IHY-1905431, CCT-UFMG].
22. *Enicospilus hawaiiensis* (Ashmead, 1900) (1♀, 1♂) **USA**, Hawaii, T.H., 7600ft, 30.vii.[19]36, E.H. Bryan, Jr. leg. [♀, BM]; *idem*, Pohakuloa, ?hu, 31.vii.[19]35 [♂, BM].
23. *Enicospilus heinrichi* Gauld & Mitchell, 1981 (1♀) **Laos**, Nam-Hou, 10.ii.[19]05, Micholitz leg. [**HOLOTYPE**, ZMHB].
24. *Enicospilus hospes* Gauld & Mitchell, 1981 (1♀) **New Guinea**, Mt. Kaindi, 2350m, 30.iv.1966, J.L. & M. Gressitt leg., Light Trap [**PARATYPE**, BM].
25. *Enicospilus kauaiensis* (Ashmead, 1900) (1♀) **USA**, Hawaii, Sandwich Is., vii.[18]96, 1912-215 [**LECTOTYPE**, B.M.Type Hym.3B1312 BMNH].
26. *Enicospilus lineatus* (Cameron, 1883) (3♀, 1♂) **USA**, Hawaii, Hana Maui, ?7.v.[19]20, E.H. Bryan, Jr. leg. [♂, BM]; Hawaii, Kapalama, Nuuanu Oahu, 17.viii.[19]29, E.H.Bryan, Jr. leg. [♀, BM]; Hawaii, Kilauea, vii.1906 [♀, BM]; Hawaii, Oahu, T. H., ix.1913, J.F.Illingworth leg. [♀, BM].
27. *Enicospilus longicornis* Ashmead, 1901 (2♀) **USA**, Hawaii, Maui I: Hleakala Nat'l Park: upper Kipahulu Valley Charlie Camp, 1450m, 28.ii–4.iii.1984, W.C. Gagné, S.Gon III leg., UV light in forest [2♀, BM].
28. *Enicospilus merion* Gauld & Mitchell, 1981 (1♂) **New Britain**, no further data [**HOLOTYPE**, ZMHB].
29. *Enicospilus molokaiensis* (Ashmead, 1900) (7♀, 2♂) **USA**, Hawaii, Haleakala, Maui, Sandwich Is., 5000ft, v.1896, Perkins leg., 1912-215 [2♀, BMNH]; Hawaii, Kauai, Alakai Swamp, Kelekua Hut, 4520', 1982, K. & E. Sattler leg. B.M.1982-342 [♀, 2♂, BMNH]; Hawaii, Kauai, Na Pali, Kona Forest Reserve, Alakai Swamp Trail, 3800', 26.vii.1982, K. & E. Sattler leg., B.M.1982-342 [3♀, BMNH]; Hawaii, Kauai, Sandwich Isl., 2–3000ft, i–ii.1897, 1912-215 [♀, **LECTOTYPE**, B.M.Type Hym.3B1311 BMNH].



30. *Enicospilus morobe* Gauld & Mitchell, 1981 (1♀, 1♂) **New Guinea**, NE Mt. Kaindi, 2360m, 2.iii.1974, J.L.Gressitt leg. [♀ ♂, **PARATYPES**, BM].
31. *Enicospilus muluensis* Gauld & Mitchell, 1981 (1♀) **Borneo**, Sarawak Nanga Pelagus nr. Kapit 180, 585m, 7–14.viii.1958, T.C.Maa leg. [**PARATYPE**, BM].
32. *Enicospilus muscus* Gauld & Mitchell, 1981 (1♀, 1♂) **New Guinea**, NE Mt. Missim, 2450–2800m, 22–30.iv.1968, J.L.Gressitt leg. [♀, **PARATYPE**, BM]; *idem*, Bulldog Rd.ci4km S Edie CK, 240m, 4–10.vii.1966, C.A.Samuels leg., Light Trap [♂, **PARATYPE**, BM].
33. *Enicospilus nigronotatus* Cameron, 1903 (1♀) **China**, Canton, Mell S.V. leg. [ZMHB].
34. *Enicospilus nigropectus* Cameron, 1903 (1♀, 1♂) **Borneo**, ?Liluas, Lam bao, 22–26.vii.[19]03, Micholiz leg. [♂, ZMHB]; Japan, Yamagata-ken, Mogami-gun, Mamurogawa-machi, 38°48'30"N; 140°48'32"E, 21.viii.2012, Y.Matsubara & K.Fukuda leg. [♀, LIBES].
35. *Enicospilus purgatus* (Say, 1835) (4♀) **Brazil**, **Paraná**, Jundiaí do Sul, PR, Fazenda Monte Verde, 06.viii.1986, Lev. Ent. Profaupar, Lâmpada [DZUP]; Umuarama, Estrada Vermelha, 28.ix–4.x.1980, A.F.Yamamoto leg., Malaise [UFMG-IHY-1905417, CCT-UFMG]; *idem*, 21–26.xii.1980 [UFMG-IHY-1905418, CCT-UFMG]; **Santa Catarina**, São Francisco do Sul, CEPA - Vila da Glória, 19–20.xii.2011, C.F.Carmo & P.G.Dias leg., luminosa [UFMG-IHY-1905416, CCT-UFMG].
36. *Enicospilus rundiensis* Bischoff, 1915 (2♂) **D.O Afrika**, West Urundi, 21.ix.1911, H.Meyer S.G. leg. [**LECTOTYPE**, ZMHB]; *idem* [**PARALECTOTYPE**, ZMHB].
37. *Enicospilus senescens* (Tosquinet, 1896) (1♂) **Togo**, no further data [**LECTOTYPE**, ZMHB].
38. *Enicospilus shikokuensis* (Uchida, 1928) (1♂) **Japan**, Nara, Obuchi-ike Park, 34°42'28"N; 135°44'41"E, 130m, 13.v.2012, Masato Ito leg. [LIBES]
39. *Enicospilus teodora* Gauld, 1988 (3♀, 3♂) **Brazil**, **Minas Gerais**, Belo Horizonte, Estação Ecológica UFMG, 11.viii.2000, A.F.Kumagai leg., Malaise [♀, UFMG-IHY -1905420, CCT-UFMG]; *idem*, 12.iv.2000 [♀, UFMG-IHY-1905419, CCT-UFMG], 19.v.2000 [♂, UFMG-IHY-1905424, CCT-UFMG], 26.i.2001 [♂, UFMG-IHY- 1905422, CCT-UFMG], 29.iii.2000 [♀, UFMG-IHY-1905421, CCT-UFMG], 5.iv.2000 [♂, UFMG-IHY-1905423, CCT-UFMG].
40. *Enicospilus trilineatus* (Brullé, 1846) (3♀, 2♂) **Brazil**, **Bahia**, Amargosa, Faz. Timbó, Serra do Timbó, 13°05'06"S; 39°38'50"W, 47m, 17.vii.2009, Calor *et al.* leg. bandeja/luz [♂, UFMG-IHY-1905429, CCT-UFMG]; **Minas Gerais**, Minas Gerais, Serra do Salitre, RPPN Cachoeira do Campo, 19°09'46.3"S; 46°33'59.7"W, 1076m, 11.x.2012, A.R.Lima & A.F.Kumagai leg., luz negra [2♀, UFMG-IHY-1905425, UFMG-IHY-1905427, CCT-UFMG]; *idem*, 12.x.2012 [♀, UFMG-IHY-1905422, CCT-UFMG], 13.x.2012 [♀, UFMG-IHY-1905426, CCT-UFMG].

41. *Enicospilus yonezawanus* (Uchida, 1928) (4♀) **New Guinea**, (NE) Lae 24km, 100m, 28.xi.1961, J.Sedlaced *leg.* [2♀, BM]; (NE) Wau, Morobe Distr., 1200m, 17.xi.1969, M. Sedlacek *leg.* [BM]; idem, 1–20.xi.1961, J.Sedlaced *leg.*, Light Trap [BM].
42. *Eremotylus aridus* (Cushman, 1947) (2♀) **USA**, Arizona, Kits Peak Rincon, Baboquivari Mts. 31°57'N, 111°33'E, 4050ft. 1–4.VIII.1916, Clark and A. N. S. P. *leg.* [PARATYPE, AMNH]; Oracle, 14 Mi. E. Arizona, 27.VII.1924, J. O. Martin *leg.* [PARATYPE, CAS]
43. *Eremotylus curvinervis* (Kriechbaumer, 1878) (2♀, 1♂) **Spain**, Sierra Morena, 1926, Seyrig *leg.* [♀, NHRS-HEVA6042, SMNH]; Sierra Morena, Fuencaliente, 11.vi.1925, Seyrig *leg.* [♀, COTYPE of *E. dryobotae*, NHRS-HEVA6043, SMNH]; Sierra Morena, El Soldado, Seyrig *leg.* [♂, COTYPE of *E. dryobotae*, NHRS-HEVA6044, SMNH];
44. *Eremotylus marginatus* (Jurine, 1807) (1♀, 1♂) **France**, Gallia meridionalis, Sichel. *leg.* [♂, NHRS-HEVA6045, SMNH]; **Germany**, no further data [♀, 11342, TYPE (There is a Type label), ZMHB].
45. *Eremotylus perdix* Gauld & Mitchell, 1981 (1♀) **India**, Waziristan, N.W. India, iv–v.1930, Rev. G. Palacios *leg.*, B.M.1931-1 [HOLOTYPE, B.M.TYPE HYM 3B.2315, BMNH].
46. *Eremotylus vitripennis* Townes, 1971 (1♀) **Argentina**, Rio Negro, Villa Regina, 7.X.1964, H. A. Piacentini *leg.* [DZUP].
47. *Euryophion ikuthanus* (Kriechbaumer, 1901) (8♀, 1♂) **Kenia**, Kibuezi, Tsavo Park, 1300m, xii.1989, K. Werner *leg.* [2♀, La Specola Firenze Hymenopter collection n. 1133 and 1137, MSNF]; Tsavo National Park, Kilaguni lodge, 30.vi.1965, R.Gregg *leg.* [♀, FMNH]; Kibweziw. F, ii.1929, Van Someren *leg.* [♂, BMNH]; **Republic of South Africa**, Natal Province, Hluhluwe village, 11.XII.1970, H. V. & D. D. Daly *leg.* U.V. light [♀, CAS]; **Somalia**, It. Mer., x.1913, Lugh *leg.* [♀, La Specola Firenze Hymenopter collection n. 1134, MSNF]; **Tanzania**, Mto Wa Mbu (Lake Manyara), 1000m, 9–25.iv.1999, L. Bartolozzi, B. Carletti, B. Cecchi & A. Sforzi *leg.* Alla luce (n° Mag. 2187) [♀, La Specola Firenze Hymenopter collection n. 1135, MSNF]; "View Point" sul Lake Manyara, lungo la strada per Karatu, 1300m, 10–25.iv.1999, L. Bartolozzi, B. Carletti, B. Cecchi & A. Sforzi *leg.* Alla luce (n° Mag. 2187) [♀, La Specola Firenze Hymenopter collection n. 1136, MSNF]; **Uganda**, Mt-Labyor, Karamoja 4-50[?iv.1950], V. G. L. van Someren collection. Brit.Mus.1959-468, Van Someren *leg.* [♀, BMNH].
48. *Euryophion nigripennis* Cameron, 1906 (11♀) **Kenya**, 160 km E. of Nairobi, on road to Mombassa, Hunter's Lodge, 02.V.1975, Victor De Masi *leg.* [2♀, CAS]; **Namibia**, Halali, 19°01'S, 16°29'E, 17.iii.1997, J. Deckert *leg.* Lux [2♀, ZMHB]; Outjo Buschfeld Park Resort, 04.02.2009 [?04.ii.2009], W. Mey *leg.* [2♀, ZMHB]; Kaokoland, 10km E. Opuwo, 22.ii.1994, F. Koch *leg.* [♀, ZMHB]; **Zambia**, N.Rhodesia, Livingstone,

- 14.xii.1941, W. Eichler *leg.* Mus.Zool.Polonicum Warszawa 30-47 [♀, MIIZ]; *idem*, xii.1941–i.1942 [2♀, MIIZ]; N.Rhodesia, Lusaka, 16.x–6.xi.1944, W. Eichler, Mus.Zool.Polonicum Warszawa 30-47 [♀, MIIZ].
49. ***Euryophion latipennis*** (Kirby, 1986) (2♀, 1♂) **Democratic Republic of Congo**, Itruri, Eldh *leg.* [♂, **ALLOTYPE** of *Thoracophion ventrator*, NHRS-HEVA6047, SMNH]; **Guinea**, Sérédou, 2.v.1976, Dr. A. Zott *leg.* [♀, ZMHB]; **Uganda**, Tororo, v.1925, Bryck *leg.* [♀, **LECTOTYPE** of *Thoracophion ventrator*, NHRS-HEVA6046, SMNH].
50. ***Heinrichiella obscura*** Gravenhorst, 1823 (2♀, 3♂) No location data, Schmiedeknecht *leg.* [♂, ZMHB]; **Austria**, Jedlesee, Wien, Mader *leg.* [♀, NHRS-HEVA6050, 2♂, NHRS-HEVA6051, NHRS-HEVA6052 SMNH]; **Croacia** [?], Susak, 25.vi.[19]85 [♀, ZMHB].
51. ***Hellwigia elegans*** Gravenhorst, 1823 (2♀, 1♂, 1?) **Austria**, Oberweiden, A. I. Mader *leg.* [?metasoma missing, NHRS-HEVA6048, SMNH]; **Spain**, Vaciamadrid, Dusmet *leg.* [♀, NHRS-HEVA6049, SMNH]; **Germany**, Halle, vii.[19]22, Fist *leg.*, 14 - 298 [♂, ZMHB]; No location data, viii.[19]84 [♀, ZMHB].
52. ***Hellwigiella dichromoptera*** (Costa, 1885) (4♀, 1♂) **Italy**, S. Giorgio Molafa, Sardinia, 24.v.[19]64, C. G. Roche *leg.* [♀, BMNH]; *idem* [♀, NHMUK 01081840, BMNH]; **Israel**, Tiberias, 200m, 22.iii.1975, K. M. Guichard *leg.* BM 1975-154 [♀, BMNH]; **Palestine**, Ein Deb [?], 4.iv.1942 [?], Iiqski-salz *leg.* Pres By Com Inst Ent BM 1956-413 [♀, BMNH]; **Morocco**, c. 15km n. Tiznit (Agadir rd), 4.iv.1983, M. Edwards *leg.* *Eucalyptus* plantation roadside Prep. gen. H37, collezione Scaramozzino [♂, BMNH].
53. ***Janzophion nebosus*** Gauld, 1985 (2♀, 4♂) **Costa Rica**, Volcan Poas NP, xii.[19]82, Janzen & Hallwachs *leg.* [♂, HOLOTYPE, BMNH]; *idem* [♂, PARATYPE, BMNH]; Volcan Poas Nat. Pk., Alajuela Pr., 2350m, 19.xii.1981, D. H. Janzen & W. Hallwachs *leg.* [♂, PARATYPE, BMNH]; Heredita Pv, Braulio Carrillo NP, 9.5km E of El Tunel, 1000m, ix–x.[19]89, Gauld *leg.* [♀, BMNH]; **Panama**, Chiriqui, Guadalupe Arriba, 2200m, 20–26.iii.1985, H. Wolda *leg.* [♀, ♂, BMNH].
54. ***Janzophion saxis*** Gauld, 1988 (4♀, 1♂) **Mexico**, Dgo. El Salto 10mi. W. 9000ft, 5.vii.1964, W. R. M. Mason [♀, HOLOTYPE, CNC]; *idem* [♀, ♂, PARATYPES, CNC]; *idem*, 30.vi.1964 [♀, PARATYPE, CNC]; *idem*, 15.vii.1964 [♀, PARATYPE, BMNH]. \*The type specimens from CNC were studied while they were in the BMNH.
55. ***Laticoleus infumatus*** Gauld & Mitchell, 1978 (1?) **Uganda**, Ruwenzori Range, Nyamgasani Valley, 8–9000ft, xii.1934–i.1935, D. R. Buxton *leg.*, B.M.E.Afr.Exp., B.M.1935-203 [?missing apex of metasoma, PARATYPE, BMNH].
56. ***Laticoleus longicornis*** Delobel, 1974 (1?missing apex of metasoma) **Madagascar**, Perinet Foret Core Est, ii.[19]39, A. Seyrig *leg.* [BMNH].

57. *Laticoleus palpalis* Gauld & Mitchell, 1978 (1?) **Sierra Leone**, Port Lokko, 10.v.[19]12, J. J. Simpson *leg.*, 1912-478 [?missing apex of metasoma, **PARATYPE**, BMNH].
58. *Laticoleus unicolor* (Szépligeti, 1908) (3♀, 3♂) **Kenya**, Kenya Colony, Naivasha, 6–10.vi.1942, H. Copley *leg.* [♀, BMNH]; Nairobi, Karen, 18.ii.1982, C. F. Dewhurst *leg.*, Light trap [♀, BMNH]; Nandi Plateau (Some forest), 5700–6200ft, 30.v–04.vi.1911, S. A. Neave *leg.*, Brit.E.Africa, 1912-193 [♂, BMNH]; **Nigeria**, Yala R., S. edge Kakumba forest, 4800–5300ft, 21–28.v.1911, S. A. Neave *leg.*, Brit.E.Africa, 1912-193 [♂, BMNH]; **Republic of South Africa**, Natal, Malvern, 1904, J. P. Cregoe *leg.*, 1904-46 [♂, BMNH]; **Tanzania**, Ilala, Maramas Dist. 14m. E. of Mumias, 4500ft, 18–21.vi.1911, S. A. Neave *leg.*, Brit.E.Africa, 1912-70 [♀, BMNH].
59. *Lepiscelus distans* (Seyrig, 1935) (4♀, 4♂) **Democratic Republic of Congo**, Tanganyika Terr.: Handenl, 350m, 25–27.iv.1957, Mission Zoolog. I.R.S.A.C. en Afrique Orientale (P.Basilewsky et N.Leleup), Coll. Mus. Congo [♀, BMNH]; Bambesa, i.1937, J. Vrydagh *leg.*, Musée du Congo [♂, BMNH]; **Ivory Coast**, Côte d'ivoire, Bingerville, vii.1962, J. Decelle *leg.*, Coll. Mus. Tervuren [♀, BMNH]; **Kenia**, Brit. E. Africa. Nandi Plateau. (some forest), 5700–6200ft, 30.v–04.vi.1911, S. A. Neave *leg.* 1912-193 [♂, BMNH]; **Tanzania**, Magara (a sul del Lake Manyara sulla strada fra Mbulu e Magugu), 1000m, 15.iv.1999, L. Bartolozzi, B. Carletti, B. Cecchi & A. Sforzi *leg.*, alla luce (n° Mag. 2187) 10–25.iv.1999, La Specola Firenze Hymenopter collection n. 1146 [♀, MSNF]; Strada Mto Wa Mbu-Karatu, 1450m, 10–25.iv.1999, L. Bartolozzi, B. Carletti, B. Cecchi & A. Sforzi *leg.*, alla luce (n° Mag. 2187) [♂, MSNF]; **Zambia**, 15km E. Lusaka, 11–21.i.1980, R. A. Beaver *leg.* [♀, ♂, BMNH].
60. *Leptophion alleni* Gauld & Mitchell, 1981 (1♀) **Brunei**, Bukit Retak, Montane Forest, 1618m, 1.x.1979, I. D. Gauld *leg.* [♀, **HOLOTYPE**, B.M.Type Hym 3B2305, BMNH].
61. *Leptophion antennatus* (Morley, 1912) (1♀) **Australia**, W. Australia, 1906, G. C. Shortridge *leg.* [♀, **HOLOTYPE**, B.M.Type Hym 3B1299, BMNH].
62. *Leptophion quorus* Gauld & Mitchell, 1981 (3♀, 1♂) **Papua New Guinea**, Wan., 1000m, x.[19]79, I. D. Gauld *leg.*, Light [♂, **HOLOTYPE**, B.M.Type Hym 3B2304, BMNH]; (NE) Mau, Morobe Distr., 1200m, 1–20.xi.[19]61, J. Sedlacek *leg.*, BISHOP, light trap [♀, **PARATYPE**, BM]; Wan., 1200m, 1.x.1955, J. & M. Sedlacek *leg.*, BISHOP [♀, **PARATYPE**, BM]; NE., Finisterre Range Saidor: Matoko Vill., 6–24.ix.[19]58, W. W. Brandt *leg.*, BISHOP [♀, **PARATYPE**, BMNH].
63. *Leptophion orientalis* (Morley, 1912) (1♀) **Taiwan**, Lixing Industry Rd, Ren' ai Township, Nantou County, 24°03'19.3"N, 121°09'18.4"E, 1500m, 7–8.v.2016, So Shimizu *et al.* *leg.*, light trap [LIBES].

64. *Leptophion* sp.1 (7♀, 2♂) **Papua New Guinea**, Bismarck Archipelago, NW. New Britain, Talassea, Narunageru road., 24.xi.1969, James E. Tobler leg., [♂, CAS]; Dutch N. Guinea, Maffin Bay, 09.vii.1944, E. S. Ross leg., [3♀, CAS]; *idem*, 10.vi.1944 [3♀, ♂, CAS]; Finschhafen, 15.iv.1944, E. S. Ross leg. [♀, CAS].
65. *Ophiogastrella nigrifrons* (Enderlein, 1921) (7♀, 9♂) **Brazil, S[anta] Catarina**, Lüderwaldt leg., Mus. Zool. Polonicum Warszawa 12/45 [♂, HOLOTYPE, Typus n. 2715, MIIZ]; Nova Teutônia, 27°11'B., 52°23'L., 02.xii.1937, F. Plaumann leg. B.M.1938-312 [♀ BMNH]; *idem*, 11.x.1967, BMNH(E)2012-144 [♂, BMNH]; *idem*, 14.x.1967, BMNH(E)2012-144 [♀ BMNH]; *idem*, 22.xi.1938, B.M.1938-312 [♀ BMNH]; *idem*, 24.x.1938, B.M.1938-682 [♀ BMNH]; *idem*, xi.1935, Brit. Mus. 1937-47 [♂, BMNH]; *idem*, xi.1969 [♂, DZUP]; *idem*, xi.1971 [♀, 3♂, DZUP]; *idem*, xi.1973 [♀, ♂, DZUP]; *idem*, xi.1976 [♀, DZUP]; *idem*, xii.1971 [♂, DZUP].
66. *Ophiogastrella nigriventris* (Enderlein, 1921) (7♀) **Ecuador**, Santa Jnez, R. Haensch S. leg., Mus. Zool. Polonicum Warszawa 12/45 [♀ HOLOTYPE, Typus n. 2714, MIIZ].
67. *Ophion cacaoi* Gauld, 1988 (2♀) **Costa Rica**, Guanacaste, Casa Mengo SW side Volcan Cacaoi, 1000m, vi.[19]87, D.H.Janzen leg. [2♀ BMNH].
68. *Ophion calliope* Gauld, 1988 (14♀, 6♂) **Costa Rica**, Alajuela Prov.: San Ramon Reserve, Rio San Lorencito, 800m, xi.1986, Chacon leg. [♀ HOLOTYPE, B.M.TYPE HYM.3B2352, BMNH]; Puntarenas Prov.: Finca Las Cruces, 6 km S of San Vito de Java, 1400m, x.1986, Eger leg. [♂, PARATYPE, BMNH]. **Brazil, Minas Gerais**, São Gonçalo do Rio Abaixo, Est. Amb. Peti, 19°53'02.2"S, 43°22'20.4"W, 29.iv.2012, A.R.Lima & P.G.Dias leg., luz [♀ UFMG-IHY-1503931, CCT-UFMG]; *idem*, 28.iv-01.v.2012, A.Lima, A.Kumagai & P.Dias leg. [♀ CCT-UFMG]; *idem*, 10-17.xii.2012 [4♀ UFMG-IHY-1529026, UFMG-IHY-1529025, UFMG-IHY-1529032, UFMG-IHY-15290327, CCT-UFMG]; *idem*, 11-18.x.2012 [♂, UFMG-IHY-1528994, CCT-UFMG]; *idem*, 9-16.xi.2012 [♂, UFMG-IHY-1529086, CCT-UFMG]; *idem*, 15.xi.2002, A.F.Kumagai leg., malaise [♂, CCT-UFMG]; Serra Caraça, 1380m, xi.1961, Kloss, Lenko, Martins & Silva leg. [♀ DZUP]; **Paraná**, Marumbi, Morretes, 500m, 17.vii.1966, Laroca, O.Mielke leg. [♀, ♂, DZUP]; **Rio Grande do Sul**, Mato Castelhanos, 23.iii.2002 [2♀, 1♂, DZUP]; **Santa Catarina**, Nova Teutonia, v.1976, F.Plaumann leg. [♀ DZUP]; São Bento do Sul, CEPA Rugendas (Sede), 26°19'24.9"S, 49°18'26.4"W, 14-15.xii.2011, P.Dias leg., Luz [♀ CCT-UFMG]; **São Paulo**, Eug. Lefevre, C. Jordão, 1200m, 28.ix.1962, L.T.F., L.T., Rabello & Dente leg. [♀ DZUP].
69. *Ophion caudatus* (Cushman, 1947) (2♀) **India**, U.P. Kholara Garhwal dist., 11009 ft., 3.viii.1958, B.S.Lamba leg. [♀ BMNH]; Zool. Suru. Ind. N Sikkim, Lachen, 2706m, 9.vi.1959, A.G.K.Menon leg. [♀ BMNH].

70. *Ophion clio* Gauld, 1988 (2♀, 1♂) **Costa Rica**, San Jose Prov., San Gerardo de Dota, Cerro de la Muerte, 2430m, 23.xii.1981, D.H.Janzen & W.Hallwachs *leg.* [♂, BMNH]; 2km E of Cerro Assunción Cerro de La Muerte, 3140m, [no further data] [♀, BMNH]; **Panamá**, Chiriqui, Guadalupe Arriba, 2200m, 2–8.v.1984, H.Wolda *leg.* [♀, BMNH].
71. *Ophion fascetious* Gauld & Mitchell, 1981 (2♀, 1♂) **Malaysia**, Sabah, Mt. Kinabalu, Lumu-Lumu, iv.[19]29, Pendlebury *leg.* [2♀, PARATYPES, BMNH]; [specimen without data] [♂, BMNH].
72. *Ophion flavidus* Brullé, 1846 (17♀, 11♂, 1?) **Brazil**, Bahia, Curaçá, Pousada Recanto Campestre, 8°59'58.7"S, 39°54'48.3"W, 415m, 03.v.2011, D.França *leg.*, Bandeja-luz [9♂, CCT–UFMG]; *idem*, 04.v.2011 [♀, ♂, CCT–UFMG]; *idem*, 05.v.2011 [♂, CCT–UFMG]; *idem*, 06.v.2011 [3♀, CCT–UFMG]; Curaçá, riacho Tio Zé, 9°07'48.1"S, 39°58'45.7"W, 415m, 05.v.2011, D.França *leg.*, Bandeja-luz [2♀, CCT–UFMG]; Santa Teresinha, Serra da Jibóia, 12°50'45"S, 39°29'05"W, 579m, 10.vi.2010, Calor *et al.* *leg.*, Bandeja-luz [3♀, CCT–UFMG]; **Ceará**, Ubajara, 3°50'50"S, 40°53'22"W, 885m, 25.iv.2012, C.F.Cardoso *leg.* [♀, CCT–UFMG]; **Goiás**, Cabeceiras, Lagoa Formosa, 27.x.1964, Exp. Dep. Zool. [♀, DZUP]; GO, Colinas do Sul, 01.xi.2007, R.B.Martins & R.M.Carmo *leg.*, CDC [4♀, CCT–UFMG]; **Rio de Janeiro**, Campos dos Goytacazes, aeroporto, 21°42'07.3"S, 41°18'25.6"W, 04.vii.2010, A.Claudio *leg.* [♀, CCT–UFMG]; RJ, Ilha Governador, 01.i.1956, C.R.Gonçalves *leg.*, [Coleção Campos Seabra] [?, metasoma missing, DZUP]; **Rondônia**, Porto Velho, linha 22, 08°58'08.4"S, 63°52'20.8"W, 101m, 30.xi.2012, J.E.Santos Jr. *leg.*, em vôo [♀, CCT–UFMG].
73. *Ophion gelus* Gauld, 1977 (1♀, 1♂) **Australia**, [no further data] [♀, ♂, BMNH].
74. *Ophion geyri* Habermehl, 1921 (1♂) **Algeria**, S.O.Algerien, Gassi Abu ca. 360km S. Ouargla, 13–14.i.[19]14, v. Geyr S.G. *leg.* [HOLOTYPE, ZMHB].
75. *Ophion similis* (Szépligeti, 1905) (3♀, 6♂) **Israel**, Hazeva, 140m, 27.iii–3.iv.[19]88, K.Guichard *leg.* [♂, BMNH]; Jericho, Wadi Kelt, 200m, 6.iii.1975, K.M.Guichard *leg.*, B.M.1975-154 [♂, BMNH]; **Jordan**, W. Rum, 27.iv.1[9]83, I.L.Hamer *leg.*, BMNH(E)2001-56 [♀, NHMUK010818042, BMNH]; **Lybia**, Cyrenaica: Agedabia, 31.iii.1958, K.M.Guichard *leg.*, B.M.1958-544 [♀, NHMUK010820018, BMNH]; **Morroco**, S. km.31 Goulimine-Tan Tan Rd., Flowery Border of wheat field, 100m, 17.iii.1974, K.M.Guichard & G.R.Else *leg.*, B.M.1974-160 [♂, NHMUK010818041, BMNH]; *idem* [♂, BMNH]; **Palestine**, Jerusalem - Jericho Road, 26.ii.[19]41, {non legible} Yadi Kollst. *leg.*, B.M.1956-413 [♂, BMNH]; Jordan, 24.ii.1942, A.L.Maghtas *leg.*, B.M.1956-413 [♀, BMNH]; Jist El Damie, Jordan Valley, 800–1000ft., 31.iii.1920, P.J.Barraud *leg.*, [Pres. by Imp.Inst.Ent.Brit.Mus. 1931-412] [♂, BMNH].

76. *Ophion ventricosus* Gravenhorst, 1829 (1♀, 1♂) **Germany**, Leipzig, 8.vi.[19]09, A.Reichert leg. [♀, ZMHB]; *idem*, 10.v.[19]13, Krieger l. leg. [♂, ZMHB].
77. *Ophion* sp.1 (1♀) **Japan**, Wakayama Pref., Kinokawa city, Kikowa, N34.2801, E135.4077, 1–31.v.2016, Takuto Hirooka leg., Light trap [LIBES].
78. *Ophion* sp.2 (16♀, 3♂) **Brazil, Paraná**, Curitiba, Bosque Capão da Imbuia, 25°26'10.4"S, 49°13'10.2"W, 17.xi.1995, A.F.Kumagai leg., malaise [♀, CCT-UFMG]; *idem*, 10.xi.1995 [♀, CCT-UFMG]; *idem*, 03.xi.1995 [♀, CCT-UFMG]; *idem*, 04.iii.2003 [♂, CCT-UFMG]; *idem*, 07.i.2003 [♂, CCT-UFMG]; **Rio Grande do Sul**, Canela, 06–12.i.1984, M.Hoffmann leg., malaise [♀, CCT-UFMG]; *idem*, 12–16.i.1984 [♀, CCT-UFMG]; *idem*, 16–20.i.1984 [2♀, CCT-UFMG]; *idem*, 21–23.i.1984 [2♀, CCT-UFMG]; *idem*, 24–26.i.1984 [2♀, CCT-UFMG]; *idem*, 26–28.i.1984 [2♀, CCT-UFMG]; *idem*, 28–30.i.1984 [2♀, CCT-UFMG]; **Santa Catarina**, Nova Teutonia, iv.1969, F. Plaumann leg. [♀, DZUP]; *idem*, ix.1967 [♂, DZUP].
79. *Ophion* sp.3 (3♀, 2♂) **Brazil, Paraná**, Morretes (IAPAR), 17–24.ix.1984, C.I.I.F., luminosa [♀, DZUP]; *idem*, 24.ix–01.x.1984 [♂, DZUP]; S. José dos Pinhais (Br 277-km54), 21–27.viii.1984, C.I.I.F., luminosa [♂, DZUP]; *idem*, 13–20.viii.1984 [♀, DZUP]; **Santa Catarina**, São Bento do Sul, CEPA Rugendas (Sede), 26°19'24.9"S, 49°18'26.4"W, 14–15.xii.2011, P.Dias leg., luz [♀, CCT-UFMG].
80. *Ophion* sp.4 (1♀) **Brazil, Paraná**, Pico Paraná, 1700m, 22.i.1970, Laroca, Becker leg. [DZUP].
81. *Ophion* sp.5 (2♀, 1♂) **Chile**, Santiago, Maipu, 06.x.1966, R.H.Gonzalez leg., Luz negra [♀, CAS]; *idem*, 18.x.1966 [♀, CAS]; Valparaiso Prov. Rio Marga Marga Los Perales, 33°09'S, 71°19'W, 330m, 13.x.1966, M.E.Irwin, E.I.Schlinger leg., at UV light [♂, CAS].
82. *Ophion* sp.6 (2♀) **Chile**, Curico Prov. Fundo La Montana, Estero La Palma at Rio Teno, 6km. E. Los Quenes , 4.i.1967, M.E.Irwin leg. [2♀, CAS].
83. *Orientospilus capitatus* Gauld & Mitchell, 1978 (1♂, 1?) **Republic of South Africa**, Vyehoekrivier, 24°40'S, 30°38'E, 18–21.xii.1910, S. A. Neave leg. [♂, HOLOTYPE, B.M.TYPE HYM 3.B.2614, BMNH]; *idem* [?metasoma missing, PARATYPE, BMNH].
84. *Orientospilus individuus* Morley, 1912 (2♀) **India**, Deesa, Rajputana, ix.1901, Col. Nurse, Brit. Mus. 1927-486 [HOLOTYPE, B.M.TYPE HYM 3.G.1226, BMNH]; Gaiha Tulla, 14.xi.1946, A. N. G. Alston leg. [BMNH].
85. *Pamophion sorus* Gauld, 1977 (1♂) **Australia**, Brisbane, i.1973, J. Sedlacek leg. [PARATYPE, BMNH].
86. *Prethophion latus* Townes, 1971 (6♀, 1♂) **Brazil, Amazonas**, Castanho-Careiro, Ramal do Panelão 03°50'42"S, 60°26'03"W, 04–05.xi.2010, J. A. Rafael, D. M. Takiya, F. F. Xavier F°, M. J. Holanda & D. M. M. Mendes

- leg.*, Armadilha luminosa móvel [♂, INPA]; Coari, Rio Urucu, prox. IMT-1, 4°49'33"S, 65°01'49"W, 17–29.ix.1995, P. F. Bührnheim & N. O. Aguiar *leg.*, À luz mista de mercúrio [♀, CZPB]; **Bahia**, Camacã, Serra Bonita, 15°23'S, 39°34'W, 800m, 12.i.2007, G. Melo *leg.*, atraídos por luz 20h–23h [♀, DZUP]; **Minas Gerais**, Serra do Salitre, RPPN Cachoeira do Campo, 19°09'45.7"S, 46°34'01.9"W, 22–24.II.2009, A. F. Kumagai *leg.*, Luminosa [2♀, CCT–UFMG]; **Pará**, Juruti, Vista Bela, Rio Mamuru, área 1, 03°07'00"S, 56°35'06.7"W, 01.x.2009, O. T. Silveira, S. S. Silva & J. Pena *leg.*, Rede entomológica [♀, MPEG].
87. ***Rhopalophion discinervus*** (Morley, 1926) (6♀, 4♂) **Republic of South Africa**, Sodwana Bay Nat[ional] P[ark], 20.xii.1992. F. Koch *leg.* [♀, ZMHB]; Northern Prov[ince], Lekgalameetse [Nature] Res[erve], 24°12'S 30°20'E, 18.xii.1995. F. Koch *leg.* [3♀, ZMHB]; Limpopo, Lekgalameetse Nat[ure] [Reserve], 21°11'S 30°21'E, 30.x–03.xi.2010 F. Koch *leg.* [2♂, ZMHB]; Mtirikiwi, Kyle Recreational Park, 20°13'S 31°00'E, 2–5.xii.1993 F. Koch *leg.* [2♀, 2♂, ZMHB].
88. ***Rhynchophion ligulifer*** (Morley, 1912) (2♀, 5♂) **Brazil**, no data [♀, HOLOTYPE, N.M.TYPE HYM. 3.G.1197, BMNH]; **Minas Gerais**, Passa Quatro, Floresta Nacional de Passa Quatro, 22°23'16"S, 44°56'27"W, 21–23.x.2014, Grandinete, Y.C. *leg.* Coleta ativa [♂, UNESP]; Rio Grande do Sul, Staudinger *leg.* [♀, ZMHB]; **Santa Catarina**, Nova Teutônia, 27°11'B., 52°53'L., xi.1935, F. Plaumann *leg.*, Brit.Mus.1937-47 [♂, BMNH]; Lüderwaldt *leg.*, Mus. Zool. Polonicum Warsawa 12/45 [♂, HOLOTYPE of *R. odontandroplox*, Typus n.2606, MIIZ]; **São Paulo**, Jundiá, Serra do Japi, 14.xii.1987, F. Frieiro Costa *leg.* [♂, CCT–UFMG]; *idem*, 07.xii.1988, R.P.Martins *leg.* Ativa (voando) [♂, CCT–UFMG].
89. ***Rhynchophion flammipennis*** (Ashmead, 1894) (5♀, 1♂) **Argentina**, no further data, ?böttcher *leg.*, Berlin, C.2, Mus. Zool. Polonicum Warsawa 6/46 ex coll. G.Heinrich [♀, MIIZ]; **USA**, Arizona, Arivaca Creek at Arivaca. Pima Co., 31.vii.1952, H.B.Leech & J.W.Green *leg.* [2♀, CAS]; Arizona: Cochise County, Cave Creek near portal, 1585m, 20.viii.1979, Edward S. Ross *leg.* [♀, CAS]; Coyote Cove, Concepcion Bay, L. Cal., 01.x.1941, Ross & Bohart *leg.* [♀, CAS]; Pescadero, L. Cal., 08.x.1941, Ross & Bohart *leg.* [♂, CAS];
90. ***Riekophion conspicuus*** (Morley, 1912) (3♂) **Australia**, Mellbourne, French, ii.1911 [♂, BMNH]; **Tasmania**, i.1911 [♂, LECTOTYPE, B.M.TYPE HYM. 3b912, BMNH]; no data [♂, PARALECTOTYPE, BMNH].
91. ***Riekophion emandibulator*** (Morley, 1912) (1♀, 1♂) no data [♂, HOLOTYPE, B.M.TYPE HYM. 3b1223, BMNH]; **Australia**, E 3 miles N. of Barrington, Q[ueensland], ?5–6.ix.1972, V. J. Robinson & V. V. Dodd *leg.* Ex. *Anthela magnifica* {Host?} / Department of Agriculture, Sydney, N.S.W. Australia C.I.E. Coll. A.8151 [♀, BMNH].



92. *Sclerophion longicornis* (Uchida, 1928) (1♀, 1♂) **India**, Zool. Suru. Ind. W Sikkim, Dentom, 1515m, 4.iv.1959, A. G. K. Menon *leg.* [♀, BMNH]; **Nepal**, Kakani, 2070m, 1–23.viii.1983, M. Allen *leg.* [♂, BMNH].
93. *Sclerophion uchidai* Gauld & Mitchell, 1981 (1♀) **India**, H. P. Ahla, 2286m, 8-25.vi.1971, Malaise trap N° Trap1 [PARATYPE, BMNH].
94. *Sicophion pleuralis* Gauld, 1979 (1♀) **Bolivia**, Unduavi / Corioco, Yungas La Paz, 3000m 1–5.i.[19]76, Luis Peña *leg.* [PARATYPE, BMNH].
95. *Simophion excarinatus* Cushman, 1947 (1♀) **USA**, California, Needles, ii–iii.1922, J. A. Kusche *leg.* [PARATYPE, CAS].
96. *Simophion melanostigma* (Cameron, 1886) (1♀, 1♂[?]) **Brazil, Mato Grosso**, Rio Juruena, BR-29, xi.1960, M. Alvarenga *leg.* [♀, DZUP]; **Panama**, V. de Chiriqui, 2–3000ft [♂(male-missing terminalia), HOLOTYPE, NHMUK010822981, B.M.Type Hym 3G 1306, BMNH].
97. *Skiapus coalescens* Morley, 1917 (1♀) **Republic of South Africa**, Stella Bush, near Durban, Natal, iv.1915, H. W. Bell Marley *leg.*, NHMUK010823044 [HOLOTYPE, B.M.Type Hym.3B1990, BMNH].
98. *Skiapus sp.1* (1♂) **Namibia**, Mahango Game Reserve, 18°14'S, 21°43'E, 2–5.iii.1994, F. Koch *leg.*, Malaise [ZMHB].
99. *Skiapus sp.2* (3♀, 3♂, 1?) **Uamgebiet**, Bosum, 1–10.vi.[19]14, Tessmann, S. *leg.* [♀, ♂, ZMHB]; *idem*, 11–20.v.[19]14 [♀, 4♂, 1?, ZMHB], 21–31.v.[19]14 [♀, ZMHB].
100. *Stauropogon excarinatus* (Cushman, 1947) (5♀, 8♂) **Brazil, Minas Gerais**, São Gonçalo do Rio Abaixo, Estação Ambiental de Peti, 19°53'02"S, 43°22'21"W, 10–17.xii.2012, A. R. Lima, A. F. Kumagai & P. G. Dias *leg.*, luminosa [♀, UFMG-IHY-1528991, ♀, UFMG-IHY-1528993, ♂, UFMG-IHY-1528992, CCT-UFMG]; *idem*, 11–18.vi.2012 [♀, UFMG-IHY-1528990, CCT-UFMG]; *idem*, 11–18.x.2012 [4♂, UFMG-IHY-1528986, UFMG-IHY-1528987, UFMG-IHY-1528988, UFMG-IHY-1528989, CCT-UFMG]; *idem*, 8-15.ii.2013 [♀, UFMG-IHY-1529101, CCT-UFMG]; *idem*, 28.iv-1.v.2012 [♂, UFMG-IHY-1528985, CCT-UFMG]; *idem*, 14–21.v.2012 [♂, UFMG-IHY-1528984, CCT-UFMG]; *idem*, 14–16.v.2010, A. R. Lima *leg.* [♂, CCT-UFMG]; *idem*, 23.x.1987 [collector unknown] [♀, CCT-UFMG].
101. *Stauropogon bombycivorus* (Gravenhorst, 1829) (2♀, 1♂) **Germany**, Bildhausen, Krs. Kissingen, 11.viii.1946, Gerd Heinrich *leg.* [♀, FMNH]; Berlin, [further data not legible] [♀, ZMHB]; **Italy / Austria**, Bozen Tirol, 1898, Friese *leg.* [♂, ZMHB].
102. *Stauropogon michelle* Lima & Kumagai, 2013 (8♀, 2♂) **Brazil, Minas Gerais**, Marliéria, Parque Estadual do Rio Doce, 12–18.viii.1978, M. A. V. D'Andretta *leg.* [♀ HOLOTYPE, UFMG-IHY-1700066]; *idem* [♀ PARATYPE, UFMG-IHY-1700073, CCT-UFMG]; *idem*, 07–15.x.1978 [PARATYPES, ♀ UFMG-IHY-1700072, ♂ UFMG-IHY-1700075, CCT-UFMG], 15–20.ix.1979 [PARATYPES, 2♀ UFMG-IHY-1700070, UFMG-IHY-1700071, CCT-UFMG], 19–25.x.1979 [PARATYPES, 3♀ UFMG-IHY-

- 1700067–69, CCT–UFMG], 20–26.x.1980 [PARATYPE, ♂ UFMG- IHY-1700075, CCT–UFMG].
103. *Stauropogon torresi* Gauld, 1977 (1♀, 1♂) **Papua New Guinea**, NE. Wau, 1200m, 11–12.iv.1964, J. & M. Sedlacek *leg.*, light trap [♂, BM]; (Noth.) Wisselmeren: 1700m. Waghete, Tigi L., 18.viii.1955, J. L. Gressitt *leg.* [♀, BM].
104. *Thyreodon atriventris* (Cresson, 1874) (3♀, 2♂) **Belize**, Cayo, Chiquibal Forest Reserve, Las Cuevas Res. Stn., vi.2002, A. Polaszek *leg.*, at light [♀, BMNH]; **Brazil, Mato Grosso**, Dourados, 27–28.XII.1976, J. Lorenzoni *leg.* [2♂, DZUP]; **Paraná**, Morretes, IAPAR, 21.xii.1984, C.I.I.F., luminosa [♀, DZUP]; São José dos Pinhais, BR277-km54, 27.viii–03.ix.1984, C.I.I.F., Luminosa [♀, DZUP].
105. *Thyreodon boliviae* Morley, 1912 (1♀, 4♂) **Peru**, Loreto, Pucallpa, v.1952, J. M. Schunke *leg.* B.M.1952-645 [♂, BMNH]; *idem*, 18.i.1962, B.M.1962-491 [♂, BMNH]; *idem*, 30.x.1962, B.M.1962-683 [♂, BMNH]; Vilcanota, Staudinger *leg.* [♀, ♂, ZMHB].
106. *Thyreodon cyaneus* Brullé, 1846 (4♀, 1♂) **Brazil, Amazonas**, Manaus, [19]99, 99-195 [♂, BMNH]; **Colombia**, La Macarena, 29.x–07.xi.1976, M. Cooper *leg.* B.M.1976-760 [♀, BMNH]; **Peru**, Loreto, Pucallpa, 11.vi.1963, J. M. Schunke *leg.* B.M.1963-565 [♀, BMNH]; *idem*, 19.ii.1962, B.M.1962-683 [♀, BMNH]; **Surinam**, Marowijne River, vii.1965, E. A. M. Gale *leg.* Cambridge Exp. B.M.1965-516 [♀, BMNH].
107. *Thyreodon fenestratus* (Taschenberg, 1875) (1♀, 1♂) **Brazil**, no further data, Sello *leg.* [♀, 11396, ZMHB]; **Minas Gerais**, Marliéria, Parque Estadual do Rio Doce, 07–15.X.1978, M. A. V. Dandretta *leg.* [♂, CCT–UFMG].
108. *Thyreodon grandis* Cresson, 1865 (2♀) **Brazil**, no further data, Sello *leg.* [ZMHB]; Jamaica, no further data, [but it was identified in i.1911 by Morley] [BMNH].
109. *Thyreodon morosus* Smith, 1879 (3♀) **Costa Rica**, Cache, H. Rogers *leg.* [HOLOTYPE, B.M.TYPE HYM. 3B1202, BMNH]; Guanacaste, Casa Mengo, SW side Volcan Cacao, 1000m, vi.[19]87, D. H. Janzen *leg.* [BMNH]; **Peru**, Marcapata, Staudinger *leg.* [ZMHB].
110. *Thyreodon ruficornis* Brullé, 1846 (4♀, 1♂) **Argentina**, Entre Rios. R. Uruguay n.e. Concordia, 12–13.i.1980, C. & M. Vardy *leg.* B.M.1980-67 [2♀, BMNH]; **Brazil**, no further data, 11400, Virmond *leg.* [♂, ZMHB]; *idem*, Sello *leg.* [♀, ZMHB]; **Rio Grande do Sul**, 1884, R. von. Ihering *leg.* 1884-16 [♀, HOLOTYPE of *T. reflexus*, B.M.TYPE HYM. 3B1198, BMNH].
111. *Thyreodon sp.1* (1♀, 2♂) **Brazil, Minas Gerais**, Barroso, Mata ciliar (margem do Rio das Mortes), 20.iii.2010, R. L. Tanque *leg.* Malaise [♀, ♂, UFLA]; *idem*, 11.xii.2010 [♂, UFLA].
112. *Trophophion tenuiceps* Cushman, 1947 (1♀) **USA**, Palm Spr[ings], Cal[ifornia], 22.III.1916, C. L. Fox *leg.* [PARATYPE, CAS].

113. *Xylophion ketus* (Gauld, 1977) (1♀, 9♂) **Australia**, Brown M[oun]t, NSW [New South Wales] 8.iii.1963, Z. Liepa *leg.* [♂, **PARATYPE**, BMNH]; Oberon, N.S.W [New South Wales] 400–500m 23-26.i[?] [♂, BMNH]; **Tasmania**, Collins Vale, Fairy Glen, 300m, i–ii.[19]83, Williams & Gauld *leg.* [♀, 5♂, BMNH]; Cardigan R. Xing, ii.83, I. Gauld *leg.* [♂, BMNH]; Forester Pna. Flinders Creek, ii.83, I. Gauld *leg.* [♂, BMNH].
114. *Xylophion xylus* (Gauld, 1977) (5♀, 3♂) **Australia**, Brown M[oun]t, NSW [New South Wales], 18.i.1961, E. F. Riek *leg.* [♂, **PARATYPE**, BMNH]; Canberra ACT, 5.iii.1958, E. F. Riek *leg.* [♀, **PARATYPE**, BMNH]; Monga, NSW [New South Wales], 24.ix.1957, E. F. Riek *leg.* [2♀, **PARATYPE**, BMNH]; NSW [New South Wales], 7 w Rosenbank, 11.i.1958 E. F. Riek *leg.* [♂, **PARATYPE**, BMNH]; NSW [New South Wales], 2km N. by E. Monga, 10.xi.1981, I.Gauld *leg.* [♂, BMNH]; **Tasmania**, E Strahan, 6.ii.1967, E. F. Riek *leg.* [♀, **PARATYPE**, BMNH]; Gt Pine Tier, 13km N.N.W. Bronte Pk, i–ii.83, I.Gauld [♂, BMNH].

#### **OUTGROUP**

##### **ANOMALONINAE:**

115. *Anomalon sinuatum* (Morley, 1912) (2♀, 4♂) **Brazil, Pará**, FLONA Carajás, S11 C, brejo 21–28.iv.2010, Kumagai/Lopes/Lima/Fonseca *leg.*, Malaise [♀, UFMG- IHY-1905373]; *idem*, S11 A, brejo [♀, UFMG-IHY-1905373]; *idem*, S11 A, mata [♀, UFMG-IHY-1905375]; *idem*, S11 D, campo, 20–27.iv.2010, Kumagai/Lima *leg.* [3♂, UFMG-IHY-1905376, UFMG-IHY-1905377, UFMG-IHY-1905378].
116. *Ophiopterus sp.1* (2♀, 2♂) **Brazil, Minas Gerais**, Belo Horizonte, Estação Ecológica-UFMG, 19°52'30"S; 43°58'20"W, 15.xii.2000, A. F. Kumagai *leg.* Malaise [♀, UFMG-IHY-1905389]; Nova Porteirinha, 15°48'55.1"S; 43°16'26.8"W, 30.viii– 06.ix.2013, N. G. Fonseca *leg.*, Malaise [♂, UFMG-IHY-1605854]; São Gonçalo do Rio Abaixo, Estação Ambiental de Peti, 19°53'14"S; 43°22'06"W, 13.vi.2003, A. F. Kumagai *leg.*, Malaise [♂, UFMG-IHY-1905390]; **Rio Grande do Sul**, Quaraí, 22.xi.1985, J.R.Cure *leg.*, Malaise [♀, UFMG-IHY-1905388].
117. *Podogaster tranae* Gauld and Bradshaw, 1997 (3♀, 2♂) **Brazil, Pará**, FLONA Carajás, N1 campo, 30.i–5.ii.2010, Kumagai/Lopes/Lima/Fonseca/Jacobi *leg.* Malaise [♀, UFMG-IHY -1905368]; *idem*, S11C mata, 21–28.iv.2010 [♀, UFMG-IHY-1905370]; *idem*, S11D campo, 20–27.iv.2010 [♂, UFMG-IHY-1905372]; *idem*, Tarzan, campo 30.i–5.ii.2010 [♀, UFMG-IHY-1905369, ♂, UFMG-IHY-1905371].

##### **CAMPOPLEGINAE:**

118. *Cryptophion espinozai* Gauld & Janzen, 1974 (4♀, 4♂) **Brazil, Minas Gerais**, MG, Belo Horizonte, Estação Ecológica - UFMG, 19°52'30"S 43°58'20"W, 21–27.iv.1992, A.F.Kumagai *leg.*, Malaise [♀, UFMG-IHY-1605021]; *idem*, 31.xii.1991–6.i.1992 [♀, UFMG-IHY-1605022]; *idem*, 29.iii–5.iv.2000 [♂, UFMG-IHY-1605023]; *idem*, 19°52'27.4"S;

43°58'24.5"W, 835m, 13–24.ii.2017 [♂, UFMG-IHY-1703201]; Nova Lima, 19°58'74"S; 43°51'22.7"W, 4–25.x.2018, A.R.Lima *leg.*, Malaise [♂, UFMG-IHY-1606416]; Ouro Preto, RPPN Quinta dos Cedros, 20°17'39.2"S; 42°34'04.6"W, 1–10.iii.2013, P. Dias & R. Arantes *leg.*, Malaise [♀, UFMG-IHY-1605030]; São Gonçalo do Rio Abaixo, Estação Ambiental Peti-Cemig 19°53'14"S, 43°22'06"W, 28.iii–4.iv.2003, A.F.Kumagai *leg.*, Malaise [♀, UFMG-IHY-1605028]; **Paraná**, Terra Boa, 25–26.xii.1983, J.A. Rafael *leg.* [♂, UFMG-IHY-1703292].

119. ***Cryptophion guilhermoi*** Gauld and Bradshaw, 1997 (4♀, 4♂) **Brazil, Minas Gerais**, Belo Horizonte, Estação Ecológica - UFMG, 19°52'34.6"S; 43°58'22.6"W, 13–24.ii.2017, AFKumagai, ARLima & PGDias *leg.*, malaise [♀, UFMG-IHY-1703207]; *idem*, 19°52'27.4"S, 43°52'24.5"W, 835m 13–23.iii.2017 [♂, UFMG-IHY-1703861]; Marliéria, Pq.Est.Rio Doce - PERD, 19°45'8.9"S; 42°37'3.3"W, 295m, 9–10.xi.2004, J.C.R.Fontenele *leg.*, Malaise [♀, UFMG-IHY-1611697]; Nova Lima, 19°58'74"S; 43°51'22.7"W, 21.ii–13.iii.2016, A.R.Lima *leg.*, Malaise [♀, UFMG-IHY-1612837]; *idem*, 25.x–8.xi.2015 [♂, UFMG-IHY-1607784]; São Gonçalo do Rio Abaixo, Estação Ambiental Peti-Cemig 19°53'14"S, 43°22'06"W, 11–18.iv.2003, AFKumagai & PGDias *leg.*, Malaise [♀, UFMG-IHY-1611700]; *idem*, 18.iv.2003, A.F.Kumagai *leg.* [♂, UFMG-IHY-1612879]; **Pará**, Canaã dos Carajás, 6°17'37"S; 49°54'47"W, 1.iii.2012, R.M.Carmo *leg.* [♂, UFMG-IHY-1307769].
120. ***Dusona sp.1*** (2♀, 3♂) **Brazil, Minas Gerais**, Marliéria, Pq.Est.Rio Doce - PERD, 19°42'01.8"S; 42°30'07.7"W, 244m, 24–31.vii.2002, J.C.R.Fontenele *leg.*, Malaise [♀, UFMG-IHY-1700464]; *idem*, 10–17.vi.2003 [♀, UFMG-IHY-1700442], 22–29.x.2005 [2♂, UFMG-IHY-1703360, UFMG-IHY-1703366]; *idem*, 19°42'01.8"S; 42°30'7.6"W, 252m, 20–27.x.2004 [♂, UFMG-IHY-1611894].

#### CREMASTINAE:

121. ***Creagrura nigripes*** Townes, 1971 (6♀, 4♂) **Brazil, Minas Gerais**, Marliéria, Pq.Est.Rio Doce - PERD, [♀, UFMG-IHY-1700122]; *idem*, 19°42'1.8"S; 42°30'7.6"W, 252m, 10–17.xi.2004, J.C.R.Fontenele *leg.*, Malaise [♂, UFMG-IHY-1611860]; *idem*, 20–27.x.2004 [2♀, UFMG-IHY-1605317, UFMG-IHY-1611903, 2♂, UFMG-IHY-1611904, UFMG-IHY-1611906]; *idem*, 19°42'01.8"S; 42°30'07.7"W, 244m, 15–22.vii.2004 [♂, UFMG-IHY-1700457]; *idem*, 19°45'08.9"S, 42°37'03.3"W, 295m, 22–29.x.2005 [♀, UFMG-IHY-1703522], 3–10.xi.2004 [♀, UFMG-IHY-1607972], 31.viii.2002 [♀, UFMG-IHY-1700669].
122. ***Eiphosoma urgulium*** Gauld, 2000 (4♀, 4♂) **Brazil, Minas Gerais**, São Gonçalo do Rio Abaixo, Estação Ambiental Peti-Cemig 19°53'14"S, 43°22'06"W, 26.vii.2002, A.F.Kumagai *leg.*, Malaise [♂, UFMG-IHY-1905387]; **Paraná**, Umuarama, Estrada Vermelha, 23°51'14.2"S; 53°20'56.8"W, 13–19.i.1980, A.F.Yamamoto *leg.*, Malaise [♀, UFMG-

IHY-1905383]; *idem*, 20–26.i.1980 [♂, UFMG-IHY-1905385], 22–29.xii.1979 [♂, UFMG-IHY-1905386], 27.i–2.ii.1980 [♀, UFMG-IHY-1905380], 3–9.ii.1980 [♀, UFMG-IHY-1905381], 6–12.i.1980 [♀, UFMG-IHY-1905382, ♂, UFMG-IHY-1905384].

#### NESOMESOCHORINAE

123. ***Nonnus* sp.1** (3♀, 3♂) **Brazil, Minas Gerais**, São Gonçalo do Rio Abaixo, Estação Ambiental Peti-Cemig 19°53'14"S, 43°22'06"W, 30.iv.2012, A.F.Kumagai *leg.*, coleta ativa [2♀, UFMG-IHY-1502343, UFMG-IHY-1502357]; *idem*, 8–15.ii.2013, luminosa [♀, UFMG-IHY-1502357]; *idem*, 19°53'14"S; 43°22'06"W, 16–23.i.2004, Malaise [♂, UFMG-IHY-1527021], 24–31.x.2003 [♂, UFMG-IHY-1524748], 20–27.ii.2004 [♂, UFMG-IHY-1527479].
124. ***Nonnus* sp.2** (3♀, 2♂) **Brazil, Minas Gerais**, São Gonçalo do Rio Abaixo, Estação Ambiental Peti-Cemig, 19°53'02"S; 43°22'21"W, 10–17.xii.2012, Lima, Kumagai & Dias *leg.*, luminosa [♀, UFMG-IHY-1528368]; **Paraná**, Curitiba, Bosque Capão da Imbuia, 25°26'9.7"S; 49°13'11.3"W, 24.xii.2002–2.i.2003, A.F.Kumagai *leg.*, Malaise [♀, UFMG-IHY-1905392, 2♂, UFMG-IHY-1905393, UFMG-IHY-1905394]; *idem*, 13.v.2003 [♀, UFMG-IHY-1905391].

#### TERSILOCHINAE:

125. ***Stethantyx lucasi*** Graf, 1980 (4♀, 5♂) **Brazil, Minas Gerais**, São Gonçalo do Rio Abaixo, Estação Ambiental de Peti, 19°52'49"S; 43°22'07"W, 13.xii.2002, A.F.Kumagai *leg.*, Malaise [♂, UFMG-IHY-1905401]; *idem*, 15.xi.2002 [2♀, UFMG-IHY-1905397, UFMG-IHY-1905398, ♂, UFMG-IHY-1905400], 22.xi.2002 [♀, UFMG-IHY-1905396, ♂, UFMG-IHY-1905399], 28.iii.2003 [♀, UFMG-IHY-1905395]; **Paraná**, Curitiba, Bosque Capão da Imbuia, 25°26'9.7"S; 49°13'11.3"W, 17.iii.1999, A.F.Kumagai *leg.*, Malaise [♂, UFMG-IHY-1905403]; *idem*, 3.ii.1999 [♂, UFMG-IHY-1905402].

## Appendix 2

Data matrix used in the morphological cladistic analysis of the Ophioninae. Characters not applicable are represented by “-” and missing information by “?”. Polymorphisms are coded as: [01] = A; [12] = B.

### CONTINUOUS CHARACTERS

	1										2													
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9				
<i>Stethantyx lucasi</i>	0.15	0.08	0.44	0.43	0.30	0.3	0.30	0.23	0.29	0.35	0	0.5	0.26	0.26	0.12	?	0.03	2	3	0.19	0.43	0.16	0.32	0.30
<i>Afrophion nubilicarpus</i>	0.06	0.17	0.04	0.48	0.44	0.39	0.78	0.44	0.42	0.48	0.64	0.15	0.38	0.28	0.13	0.2	0.17	2	6-8	0.2	0.37	0.2	0.34	0.86
<i>Agatophiona fulvicornis</i>	0.18	0.08	0.32	0.48	0.30	0.32	0.60	0.27	0.32	0.49	0.63	0.26	0.29	0.27	0.15	0.17	0.16	4	7-8	0.2	0.35	0.17	0.27	0.49
<i>Alrophion atahualpai</i>	0.1	0.12	0.07	0.43	0.46	0.37	0.78	0.33	0.34	0.49	0.63	0.24	0.23	0.27	0.13	0.2	0.18	3	6	0.22	0.33	0.2	0.35	0.78
<i>Alrophion politus</i>	0.06	0.14	0.15	0.44	0.43	0.4	0.75	0.33	0.33	0.46	0.64	0.2	0.23	0.27	0.14	0.24	0.2	3-5	6-8	0.21	0.32	0.17	0.34	0.92
<i>Anomalon sinuatum</i>	0.1	0.08	0.32	0.36	0.51	0.37	0.64	0.4	0.43	0.38	0.63	0.18	0.48	0.23	0.18	?	0.13	4	5	0.2	0.25	0.18	0.39	0.80
<i>Barytatocephalus mocsaryi</i>	0.34	0.05	0.57	0.43	0.35	0.31	0.74	0.32	0.32	0.19	0.62	0.07	0.28	0.24	0.22	0.19	0.12	2-4	5	0.23	0.36	0.19	0.3	0.52
<i>Creagrura nigripes</i>	0.3	0.08	0.35	0.38	0.54	0.28	0.78	0.41	0.48	0.57	0.47	0.12	0.48	0.26	0.15	?	0.12	1	4	0.2	0.24	0.21	0.41	0.78
<i>Cryptophion espinozai</i>	0.24	0.09	0.25	0.38	0.30	0.26	0.54	0.26	0.35	0.47	0.4	0.21	0.36	0.24	0.2	?	0.15	1	7	0.23	0.43	0.13	0.3	0.85
<i>Cryptophion guilhermoi</i>	0.23	0.09	0.25	0.39	0.30	0.26	0.54	0.27	0.33	0.47	0.34	0.27	0.37	0.24	0.2	?	0.13	1	7	0.23	0.45	0.15	0.27	0.89
<i>Dicamptus bantu</i>	0.14	0.18	0.12	0.47	0.49	0.36	0.68	0.33	0.38	0.27	0.65	0.23	0.39	0.28	0.19	0.54	0.17	1	6	0.24	0.35	0.21	0.35	0.70
<i>Dicamptus neavei</i>	0.24	0.06	0.48	0.52	0.27	0.33	0.85	0.18	0.26	0.35	0.61	0.12	0.31	0.26	0.23	0.47	0.13	2	9-10	0.23	0.36	0.18	0.32	0.51
<i>Dicamptus nigropictus</i>	0.05	0.24	0.05	0.43	0.43	0.33	0.80	0.28	0.32	0.41	0.65	0.27	0.35	0.28	0.16	0.37	0.14	?	9	0.23	0.34	0.19	0.35	0.66
<i>Dicamptus sinuatus</i>	0.09	0.20	0.02	0.52	0.35	0.33	0.86	0.28	0.31	0.34	0.64	0.26	0.33	0.28	0.18	0.58	0.15	1	10-11	0.23	0.31	0.22	0.36	0.70
<i>Dicamptus zoracis</i>	0.08	0.23	0.02	0.54	0.39	0.32	0.83	0.29	0.33	0.37	0.66	0.21	0.31	0.29	0.16	0.59	0.14	?	11-13	0.24	0.28	0.23	0.39	0.82
<i>Dictyonotus nigrocyaneus</i>	0.26	0.07	0.48	0.54	0.19	0.37	1.04	0.24	0.29	0.18	0.73	0.27	0.37	0.26	0.14	0.19	0.16	?	10-11	0.22	0.41	0.15	0.29	0.23
<i>Dictyonotus purpurascens</i>	0.22	0.06	0.48	0.54	0.23	0.34	1.04	0.22	0.25	0.22	0.71	0.23	0.32	0.26	0.16	0.17	0.15	?	8-14	0.23	0.39	0.19	0.37	0.52
<i>Dusona</i> sp1	0.13	0.10	0.26	0.48	0.30	0.28	0.72	0.28	0.36	0.37	0.22	0.24	0.38	0.26	0.19	0.7	0.13	4	6-8	0.22	0.44	0.18	0.32	0.51
<i>Eiphosoma urgulium</i>	0.21	0.08	0.32	0.39	0.48	0.31	0.58	0.36	0.48	0.72	0.49	0.08	0.49	0.24	0.16	?	?	1	4-5	0.22	0.26	0.22	0.28	0.78
<i>Enicospilus argus</i>	0.09	0.21	0.06	0.43	0.46	0.43	0.70	0.26	0.33	0.18	0.63	0.1	0.34	0.28	0.21	0.6	0.15	4-5	7-8	0.24	0.29	0.22	0.43	0.91
<i>Enicospilus congoensis</i>	0.12	0.20	0.05	0.46	0.51	0.43	0.85	0.28	0.32	0.27	0.64	0.24	0.4	0.28	0.2	0.57	0.16	3	6	0.24	0.3	0.22	0.35	0.82
<i>Enicospilus diae</i>	0.13	0.19	0.03	0.51	0.50	0.41	0.82	0.31	0.40	0.23	0.64	0.13	0.36	0.28	0.2	0.54	0.16	3	8-9	0.24	0.3	0.22	0.41	0.86
<i>Enicospilus dryoperus</i>	0.16	0.18	0.06	0.42	0.47	0.36	0.72	0.25	0.31	0.35	0.59	0.23	0.29	0.28	0.2	0.79	0.16	2-4	6	0.24	0.3	0.22	0.43	0.84
<i>Enicospilus dryas</i>	0.15	0.19	0.04	0.51	0.53	0.35	0.70	0.32	?	0.45	0.6	0.09	0.24	0.28	0.17	0.6	0.14	3	6	0.24	0.32	0.24	0.34	0.89
<i>Enicospilus dubius</i>	0.11	0.20	0.03	0.47	0.57	0.39	0.70	0.3	0.33	0.43	0.6	0.25	0.38	0.29	0.21	0.49	0.15	3	6-7	0.24	0.31	0.22	0.37	0.84
<i>Enicospilus enormous</i>	0.13	0.22	0.02	0.54	0.51	0.35	0.70	0.23	0.31	0.29	0.64	0.19	0.37	0.28	0.2	0.66	0.15	2	10-11	0.24	0.28	0.22	0.42	0.85
<i>Enicospilus expeditus</i>	0.11	0.20	0.04	0.49	0.56	0.38	0.72	0.29	0.32	0.35	0.62	0.17	0.36	0.29	0.21	0.52	0.16	3	6-7	0.24	0.32	0.22	0.37	0.84
<i>Enicospilus flavoscutellatus</i>	0.13	0.20	0.03	0.44	0.52	0.38	0.78	0.29	0.34	0.26	0.62	0.15	0.33	0.29	0.2	0.55	0.16	3-5	7-8	0.24	0.3	0.22	0.37	0.89
<i>Enicospilus hawaiiensis</i>	0.12	0.17	0.05	0.46	0.52	0.37	0.71	0.27	0.37	0.38	0.62	0.14	0.32	0.27	0.19	0.54	0.14	1-2	5-6	0.24	0.33	0.22	0.38	0.74
<i>Enicospilus heinrichi</i>	0.12	0.20	0.02	0.46	0.56	0.35	0.78	0.29	0.33	0.13	0.61	0.13	0.39	0.28	0.21	0.46	0.15	3-4	7	0.24	0.31	0.25	0.37	0.89
<i>Enicospilus hospes</i>	0.12	0.20	0.04	0.47	0.53	0.38	0.78	?	?	0.29	0.61	0.15	0.32	0.29	0.17	0.54	0.16	5	6-7	0.24	0.3	0.22	0.33	0.86
<i>Enicospilus kauaiensis</i>	0.2	0.09	0.28	0.4	0.48	0.36	0.67	?	?	0.2	0.64	0.1	0.3	0.27	0.2	0.41	0.16	2-3	7	0.21	0.39	0.16	0.28	0.45
<i>Enicospilus lineatus</i>	0.12	0.19	0.06	0.41	0.51	0.37	0.78	0.27	0.33	0.22	0.63	0.14	0.33	0.28	0.18	0.44	0.16	2	6	0.24	0.33	0.21	0.37	0.66
<i>Enicospilus longicornis</i>	0.14	0.18	0.05	0.47	0.44	0.38	0.83	0.27	0.32	0.26	0.63	0.19	0.36	0.28	0.2	0.52	0.14	2-4	8-9	0.23	0.29	0.22	0.35	0.78
<i>Enicospilus merion</i>	0.11	0.20	0.02	0.47	0.62	0.34	0.88	0.35	0.38	0.23	0.61	0.05	0.26	0.28	0.23	0.62	0.17	2-3	6	0.24	0.3	0.22	0.39	0.86
<i>Enicospilus molokaiensis</i>	0.14	0.13	0.13	0.39	0.50	0.32	0.62	0.27	0.30	0.22	0.65	0.04	0.31	0.28	0.2	0.52	0.16	3	8	0.22	0.36	0.18	0.32	0.43
<i>Enicospilus morobe</i>	0.14	0.22	0.02	0.51	0.48	0.33	0.78	0.31	0.39	0.33	0.65	0.16	0.4	0.29	0.2	0.78	0.13	2-3	7-8	0.24	0.28	0.21	0.4	1.00
<i>Enicospilus muluensis</i>	0.15	0.19	0.06	0.48	0.58	0.42	0.74	0.3	0.34	0.26	0.6	0.11	0.32	0.28	0.23	0.46	0.15	3-4	6	0.24	0.3	0.22	0.39	0.89
<i>Enicospilus muscus</i>	0.13	0.21	0.03	0.51	0.54	0.35	0.70	0.33	0.37	0.39	0.61	0.14	0.32	0.29	0.16	0.43	0.16	2-4	6-7	0.24	0.31	0.22	0.37	0.89
<i>Enicospilus nigronotatus</i>	0.11	0.25	0.02	0.51	0.46	0.38	0.85	0.28	?	0.36	0.66	0.24	0.34	0.29	0.19	0.71	0.14	4	10-11	0.25	0.27	0.22	0.41	0.92
<i>Enicospilus nigropectus</i>	0.19	0.17	0.05	0.51	0.58	0.42	0.74	0.31	0.36	0.25	0.6	0.12	0.31	0.28	0.23	0.48	0.16	2-3	6-7	0.24	0.31	0.22	0.38	0.84
<i>Enicospilus purgatus</i>	0.15	0.19	0.07	0.48	0.51	0.41	0.65	0.29	0.34	0.18	0.62	0.14	0.35	0.28	0.22	0.51	0.15	3	6-7	0.24	0.31	0.22	0.37	0.89
<i>Enicospilus rundiensis</i>	0.14	0.18	0.06	0.45	0.43	0.42	0.74	0.32	0.39	0.24	0.63	0.13	0.38	0.28	0.2	0.57	0.15	2-3	7	0.24	0.31	0.22	0.39	0.86
<i>Enicospilus senescens</i>	0.12	0.21	0.02	0.47	0.52	0.38	0.85	0.26	0.36	0.36	0.66	0.3	0.41	0.28	0.19	0.61	0.16	3	6	0.24	0.32	0.22	0.34	0.78
<i>Enicospilus shikokuensis</i>	0.12	0.16	0.07	0.51	0.46	0.38	0.82	0.34	0.37	0.19	0.63	0.14	0.33	0.29	0.22	0.51	0.18	4-5	8	0.22	0.31	0.22	0.36	0.80
<i>Enicospilus teodora</i>	0.15	0.17	0.06	0.51	0.64	0.33	0.78	0.28	0.32	0.44	0.61	0.09	0.34	0.29	0.22	0.49	0.16	3-4	6-7	0.23	0.25	0.22	0.41	0.84
<i>Enicospilus trilineatus</i>	0.16	0.19	0.06	0.48	0.57	0.41	0.66	0.25	0.31	0.24	0.62	0.15	0.33	0.28	0.22	0.76	0.17	2-3	7-8	0.25	0.31	0.22	0.39	0.86
<i>Enicospilus yonezawanus</i>	0.16	0.20	0.05	0.47	0.53	0.42	0.78	0.33	0.37	0.14	0.61	0.15	0.36	0.28	0.22	0.57	0.14	2-3	6	0.24	0.31	0.22	0.37	0.84
<i>Eremotylus aridus</i>	0.1	0.15	0.12	0.4	0.40	0.33	0.74	0.25	0.33	0.51	0.62	0.18	0.35	0.26	0.2	0.3	0.21	1-2	5-6	0.22	0.34	0.19	0.34	0.64
<i>Eremotylus curvinervis</i>	0.12	0.17	0.09	0.48	0.42	0.36	0.93	0.31	0.34	0.53	0.62	0.18	0.37	0.27	0.16	0.37	0.16	2-4	6-7	0.2	0.32	0.19	0.35	0.70
<i>Eremotylus marginatus</i>	0.17	0.13	0.14	0.46	0.30	0.41	0.70	0.28	0.30	0.45	0.64	0.13	0.33	0.28	0.19	0.37	0.19	3-4	7-9	0.22	0.32	0.18	0.34	0.69
<i>Eremotylus perdix</i>	0.1	0.16	0.07	0.45	0.46	0.39	0.76	0.33	0.35	0.38	0.63	0.17	0.38	0.27	0.17	0.2	0.15	3-4	5-6	0.22	0.33	0.19	0.34	0.78

	1														2									
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
<i>Janzophion nebosus</i>	0.15	0.23	0.04	0.51	0.54	0.37	0.63	0.27	0.32	0.29	0.65	0.18	0.33	0.29	0.1	0.72	0.15	?	7	0.23	0.3	0.23	0.35	0.91
<i>Janzophion saxos</i>	0.1	0.20	0.02	0.46	0.53	0.34	0.78	0.35	0.34	0.26	0.63	0.25	0.32	0.28	0.11	0.6	0.18	2	7-8	0.23	0.35	0.23	0.33	0.84
<i>Laticoleus infumatus</i>	0.16	0.13	0.08	0.51	0.62	0.33	0.54	?	?	0.45	0.58	0.25	0.27	0.27	0.13	0.46	0.2	2	5-6	0.22	0.3	0.2	0.36	0.82
<i>Laticoleus longicornis</i>	0.1	0.20	0.02	0.47	0.57	0.35	0.78	0.38	?	0.25	0.62	0.23	0.28	0.29	0.14	0.54	0.29	2-3	5	0.22	0.3	0.23	0.33	0.82
<i>Laticoleus palpalis</i>	0.1	0.20	0.02	0.45	0.62	0.37	0.68	0.35	?	0.36	0.64	0.31	0.36	0.28	0.18	0.43	0.24	?	6	0.21	?	?	?	?
<i>Laticoleus unicolor</i>	0.06	0.19	0.15	?	?	0.37	0.81	?	0.38	0.42	0.61	0.2	0.33	0.27	0.17	0.58	0.15	2-3	5	0.22	0.31	0.19	0.38	0.74
<i>Lepiscelus distans</i>	0.04	0.19	0.02	0.45	0.44	0.42	0.87	0.34	0.37	0.27	0.64	0.48	0.42	0.28	0.15	0.18	0.17	?	5-6	0.24	0.3	0.2	0.34	0.70
<i>Leptophion alleni</i>	0.11	0.19	?	0.51	0.53	0.35	0.73	?	?	0.37	0.66	0.1	0.27	0.29	0.15	0.35	0.18	1-2	5	0.23	0.29	0.2	0.35	0.86
<i>Leptophion antennatus</i>	0.09	0.19	0.07	0.47	0.49	0.37	0.64	0.34	?	0.3	0.62	0.08	0.32	0.27	0.16	0.48	0.15	2	4-5	0.21	0.29	0.22	0.34	0.94
<i>Leptophion orientalis</i>	0.1	0.20	0.05	0.51	0.48	0.37	0.81	0.34	0.31	0.39	0.65	0.1	0.29	0.28	0.14	0.37	0.24	2	6	0.23	0.3	0.2	0.35	0.84
<i>Leptophion quorus</i>	0.1	0.19	0.04	0.52	0.48	0.42	0.81	0.32	0.33	0.36	0.67	0.08	0.26	0.28	0.14	0.43	0.18	2-3	5	0.23	0.3	0.22	0.34	0.87
<i>Leptophion sp1</i>	0.11	0.18	0.04	0.54	0.51	0.38	0.75	0.34	0.32	0.33	0.64	0.1	0.25	0.28	0.16	0.24	0.27	2	5	0.23	0.3	0.2	0.35	0.78
<i>Nonnus sp1</i>	0.09	0.09	0.28	0.34	0.59	0.23	1.04	0.54	0.52	0.8	0.46	0.2	0.32	0.27	0.18	0.68	0.14	2	12	0.17	0.24	0.18	0.44	0.89
<i>Nonnus sp2</i>	0.09	0.09	0.28	0.35	0.54	0.23	0.91	0.48	0.52	0.75	0.5	0.21	0.32	0.27	0.17	0.64	0.12	2	12	0.18	0.26	0.17	0.42	0.82
<i>Ophiogastrella nigrifons</i>	0.12	0.17	0.08	0.48	0.50	0.35	0.72	0.29	0.34	0.42	0.61	0.12	0.3	0.28	0.18	0.42	0.15	2-3	5	0.22	0.34	0.19	0.33	0.69
<i>Ophiogastrella nigriventris</i>	0.1	0.18	0.04	0.45	?	0.42	0.90	?	?	0.3	0.62	0.13	0.29	0.29	0.16	0.52	0.15	2	4-5	0.23	0.33	0.21	0.37	0.69
<i>Ophion cacaui</i>	0.09	0.16	0.05	0.48	0.36	0.37	0.57	0.36	0.37	0.46	0.65	0.2	0.31	0.28	0.12	0.25	0.23	3-4	6-7	0.21	0.35	0.17	0.32	0.60
<i>Ophion calliope</i>	0.08	0.16	0.04	0.43	0.44	0.37	0.62	0.27	0.32	0.46	0.67	0.22	0.34	0.29	0.13	0.34	0.22	4-6	9	0.21	0.35	0.18	0.3	0.58
<i>Ophion caudatus</i>	0.18	0.16	0.05	0.48	0.46	0.39	0.73	0.29	0.35	0.55	0.62	0.16	0.33	0.28	0.11	0.31	0.22	4	9-11	0.21	0.37	0.16	0.32	0.57
<i>Ophion clio</i>	0.08	0.18	0.02	0.48	0.40	0.37	0.70	0.3	0.32	0.46	0.64	0.21	0.37	0.28	0.1	0.31	0.21	5-7	9	0.22	0.36	0.18	0.3	0.69
<i>Ophion fascetiosus</i>	0.08	0.18	0.02	0.46	0.49	0.41	0.79	0.28	0.34	0.54	0.63	0.2	0.32	0.28	0.15	0.32	0.26	3	7	0.22	0.33	?	0.34	0.73
<i>Ophion flavidus</i>	0.04	0.18	0.02	0.44	0.43	0.42	0.74	0.33	0.39	0.51	0.62	0.23	0.32	0.27	0.15	0.54	0.28	2-4	6-7	0.21	0.36	0.17	0.32	0.64
<i>Ophion gelus</i>	0.51	0.15	0.06	0.47	0.39	0.34	0.81	0.39	0.37	0.48	0.64	0.14	0.32	0.27	0.15	0.43	0.17	5	5-7	0.21	0.34	0.19	0.31	0.76
<i>Ophion geyri</i>	0.19	0.12	0.2	0.43	0.48	0.39	0.83	0.29	0.33	0.52	0.66	0.19	0.33	0.24	0.13	0.24	0.13	6-7	9	0.2	0.35	0.16	0.3	0.46
<i>Ophion similis</i>	0.39	0.07	0.46	0.59	0.19	0.34	0.74	0.28	0.32	0.54	0.7	0.24	0.33	0.24	0.19	0.22	0.14	6-9	9	0.22	0.43	0.16	0.26	0.43
<i>Ophion sp1</i>	0.08	0.12	0.06	0.41	0.39	0.36	0.74	0.32	0.34	0.52	0.62	0.18	0.31	0.27	0.11	0.37	0.22	7-8	7-8	0.22	0.38	0.16	0.32	0.54
<i>Ophion sp2</i>	0.09	0.16	0.05	0.46	0.48	0.4	0.90	0.33	0.37	0.49	0.64	0.2	0.36	0.29	0.12	0.28	0.24	4-7	8-10	0.22	0.37	0.16	0.32	0.69
<i>Ophion sp3</i>	0.08	0.16	0.07	0.48	0.43	0.43	0.70	0.27	0.31	0.52	0.63	0.27	0.32	0.28	0.12	0.28	0.26	4-5	9	0.21	0.34	0.16	0.31	0.74
<i>Ophion sp4</i>	0.25	0.10	0.26	0.48	0.39	0.38	0.68	0.31	0.37	0.36	0.68	0.22	0.35	0.28	0.13	0.2	0.26	4-5	9	0.22	0.36	0.18	0.31	0.69
<i>Ophion sp5</i>	0.08	0.14	0.08	0.47	0.45	0.4	0.70	0.36	0.37	0.57	0.62	0.15	0.35	0.28	0.12	0.33	0.26	3-4	9	0.21	0.37	0.17	0.31	0.60
<i>Ophion sp6</i>	0.08	0.15	0.05	0.48	0.43	0.4	0.73	0.35	0.34	0.48	0.64	0.19	0.35	0.27	0.14	0.39	0.21	4-7	7	0.22	0.36	0.19	0.31	0.69
<i>Ophion ventricosus</i>	0.13	0.12	0.11	0.46	0.32	0.36	0.89	0.31	0.30	0.28	0.66	0.16	0.32	0.26	0.17	0.22	0.19	1-3	8-10	0.2	0.37	0.16	0.28	0.54
<i>Ophiopteris sp1</i>	0.11	0.09	0.4	0.47	0.43	0.29	0.62	0.33	0.46	0.34	0.68	0.18	0.3	0.27	0.21	?	0.15	4-5	7	0.22	0.26	0.21	0.46	0.89
<i>Orientospilus capitatus</i>	0.24	0.10	0.27	0.44	0.30	0.34	1.00	0.21	?	0.56	0.62	0.2	0.31	0.24	0.2	0.38	0.17	4-5	8-9	0.22	0.36	0.17	0.35	0.62
<i>Orientospilus individuus</i>	0.2	0.12	0.2	0.5	0.29	0.32	0.97	0.26	?	0.41	0.66	0.13	0.32	0.24	0.19	0.36	0.14	3	6-7	0.23	0.37	0.18	0.35	0.59
<i>Pamophion sorus</i>	0.11	0.21	0.03	0.41	0.49	0.35	0.85	0.36	?	0.31	0.66	0.16	0.3	0.29	0.16	0.47	0.18	3	6	0.21	0.32	0.17	0.32	0.78
<i>Podogaster tranae</i>	0.06	0.09	0.3	0.45	0.57	0.32	0.48	0.32	0.45	0.83	0.54	?	0.38	0.24	0.16	?	?	3-5	4	0.27	0.28	0.23	0.47	0.78
<i>Prethophion latus</i>	0.06	0.19	0.04	0.44	0.44	0.42	0.68	0.24	0.28	0.31	0.67	0.09	0.35	0.28	0.15	0.26	0.17	?	8-9	0.21	0.35	0.16	0.3	0.54
<i>Rhopalophion discinervus</i>	0.08	0.19	0.02	0.46	0.58	0.39	0.60	0.31	0.34	0.54	0.64	0.12	0.28	0.28	0.15	0.5	0.17	3-4	5-6	0.22	0.35	0.19	0.3	0.64
<i>Rhynchophion ligulifer</i>	0.22	0.09	0.38	0.5	0.24	0.39	1.02	0.19	0.28	0.09	0.67	0.22	0.36	0.23	0.14	0.08	0.15	?	13	0.23	0.46	0.18	0.27	0.43
<i>Rhynchophion flammipennis</i>	0.24	0.08	0.45	0.54	0.22	0.34	0.90	0.23	0.30	0.3	0.69	0.19	0.31	0.22	0.14	0.12	0.14	?	14	0.23	0.45	0.15	0.25	0.43
<i>Riekophion conspicuus</i>	0.15	0.10	0.2	0.5	0.39	0.36	0.79	0.31	?	0.29	0.63	0.13	0.3	0.27	0.22	0.26	0.23	4	7	0.22	0.31	0.19	0.35	0.80
<i>Riekophion emandibulator</i>	0.07	0.21	0.02	0.5	0.51	0.36	0.66	0.33	?	0.16	0.62	0.29	0.42	0.28	0.2	0.39	0.16	?	8-9	0.2	0.32	0.18	0.32	0.89
<i>Sclerophion longicornis</i>	0.11	0.16	0.15	0.42	0.53	0.33	0.70	0.32	0.34	0.41	0.61	0.12	0.29	0.28	0.15	0.31	0.24	2	5	0.2	0.32	0.2	0.33	0.84
<i>Sclerophion uchidai</i>	0.06	0.19	0.06	0.38	0.61	0.36	0.70	0.33	0.32	0.43	0.62	0.1	0.27	0.28	0.14	0.34	0.2	2	6-7	0.21	0.33	0.2	0.34	0.84
<i>Sicophion pleuralis</i>	0.16	0.19	0.06	0.54	0.63	0.48	0.71	0.23	?	0.35	0.66	0.29	0.38	0.24	0.16	0.08	0.11	5	7	0.24	0.28	0.21	0.34	0.78
<i>Simophion exaristatus</i>	0.1	0.12	0.23	0.47	0.44	0.36	0.78	0.39	0.36	0.48	0.63	0.18	0.33	0.26	0.21	0.26	0.17	3	7	0.2	0.37	0.18	0.3	0.36
<i>Simophion melanostigma</i>	0.05	0.18	0.03	0.47	0.52	0.41	0.85	0.32	?	0.34	0.63	0.2	0.32	0.29	0.13	0.48	0.15	2	6	0.19	0.31	0.18	0.33	0.70
<i>Skiapus coalescens</i>	0.21	0.08	0.3	0.55	0.35	0.3	0.78	?	0.64	0.4	0.57	0.22	0.3	0.23	0.16	0.11	0.21	3-4	8-9	0.24	0.38	0.21	0.4	0.46
<i>Skiapus sp1</i>	0.2	0.07	0.32	0.48	0.34	0.3	0.61	0.27	0.51	0.32	0.57	0.29	0.33	0.23	0.14	0.08	0.23	4	6	0.24	0.37	0.2	0.41	0.46
<i>Skiapus sp2</i>	0.25	0.07	0.3	0.5	0.40	0.3	0.72	0.3	0.54	0.3	0.57	0.27	0.28	0.23	0.15	0.15	0.18	4	6	0.24	0.39	0.19	0.43	0.40
<i>Stauropoctonus bombycivorus</i>	0.13	0.24	0.02	0.45	0.40	0.42	0.86	0.3	0.39	0.22	0.66	0.2	0.3	0.28	0.13	0.28	0.13	?	8-13	0.24	0.3	0.2	0.37	0.78
<i>Stauropoctonus exaristatus</i>	0.1	0.17	0.02	0.47	0.52	0.3	0.64	0.29	0.34	0.22	0.67	0.17	0.32	0.29	0.12	0.59	0.18	?	3-6	0.24	0.29	0.22	0.37	0.66
<i>Stauropoctonus michelle</i>	0.08	0.19	0.02	0.49	0.42	0.3	0.85	0.3	0.33	0.25	0.7													











	1									1									1								
	4									5									6								
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	0	1	2	3
<i>Stethantyx lucasi</i>	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	3	0	1	1	0	1	1	0	1	1	
<i>Afrophion nubilicarpus</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Agatophiona fulvicornis</i>	0	0	0	0	0	2	0	1	1	0	1	1	1	?	?	?	3	0	0	0	1	0	1	0	1	1	
<i>Alrophion atahualpai</i>	0	0	0	0	0	1	0	0	1	0	1	0	1	?	?	?	0	0	0	0	0	0	0	0	1	1	
<i>Alrophion politus</i>	0	0	0	0	1	3	0	0	1	0	1	1	0	?	1	?	0	0	0	0	0	0	0	0	1	1	
<i>Anomalon sinuatum</i>	0	0	0	0	0	0	0	0	0	1	0	-	0	0	1	1	0	1	1	1	0	0	1	1	0	0	1
<i>Barytaocephalus mocsaryi</i>	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	2	?	?	?	?	?	?	?	?	?	
<i>Creagrura nigripes</i>	1	0	0	0	0	4	0	0	0	1	1	1	1	0	1	1	3	1	1	0	0	2	0	0	0	1	
<i>Cryptophion espinozai</i>	1	0	0	0	0	0	0	2	0	1	1	0	1	0	1	1	0	1	1	0	0	0	0	1	0	1	
<i>Cryptophion guilhermoi</i>	1	0	0	0	0	0	0	2	0	1	1	0	1	0	1	1	0	1	1	0	0	1	0	0	0	1	
<i>Dicamptus bantu</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	
<i>Dicamptus heavei</i>	1	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	1	1	
<i>Dicamptus nigropictus</i>	-	0	0	0	0	0	0	1	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	1	1	
<i>Dicamptus sinuatus</i>	1	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	0	0	0	0	0	0	0	0	1	1	
<i>Dicamptus zoracius</i>	-	0	0	0	0	1	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	1	1	
<i>Dictyonotus nigrocyaneus</i>	-	0	0	0	0	1	0	2	0	1	1	1	1	?	?	?	0	0	0	0	0	0	0	0	1	1	
<i>Dictyonotus purpurascens</i>	-	0	0	0	0	0	1	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	1	1	
<i>Dusona sp1</i>	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	1	1	
<i>Eiphosoma urgulium</i>	1	0	0	0	0	4	0	0	0	1	0	-	0	0	1	1	0	1	1	1	0	0	1	0	0	1	
<i>Enicospilus argus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus congoensis</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus diae</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus dnopherus</i>	0	0	0	0	1	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus dryas</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus dubius</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus enormous</i>	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus expeditus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus flavoscutellatus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus hawaiiensis</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	1	0	0	0	0	0	1	
<i>Enicospilus heinrichi</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus hospes</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus kauaiensis</i>	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	1	
<i>Enicospilus lineatus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus longicornis</i>	0	1	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus merion</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus molokaiensis</i>	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	1	1	
<i>Enicospilus morobe</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus muluensis</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus muscus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus nigronotatus</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus nigropectus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus purgatus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Enicospilus rundiensis</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus senescens</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus shikokuensis</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus teodora</i>	0	0	2	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	
<i>Enicospilus trilineatus</i>	0	0	2	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	
<i>Enicospilus yonezawanus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Eremotylus aridus</i>	0	0	0	0	1	1	0	0	1	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Eremotylus curvinervis</i>	0	0	0	0	1	1	0	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	
<i>Eremotylus marginatus</i>	0	0	0	0	1	2	0	0	1	0	1	1	1	?	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Eremotylus perdix</i>	0	0	0	0	1	3	0	0	1	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Eremotylus vitripennis</i>	0	0	0	0	1	3	0	0	1	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Euryophion ikuthanus</i>	-	0	0	0	1	2	2	0	0	0	-	1	?	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Euryophion latipennis</i>	-	0	0	0	1	0	0	2	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Euryophion nigripennis</i>	-	0	0	0	1	0	0	2	0	1	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Heinrichiella obscura</i>	0	1	0	1	1	1	0	1	0	0	1	0	1	0	1	?	0	1	0	0	0	0	0	0	0	1	
<i>Hellwigia elegans</i>	-	1	0	1	1	0	0	0	0	0	1	0	1	?	?	?	4	1	0	0	0	0	0	0	0	1	
<i>Hellwigiaella dichromoptera</i>	0	0	0	0	0	2	0	0	1	1	1	1	1	?	?	?	0	0	0	0	0	0	0	0	0	1	
<i>Janzophion nebosus</i>	-	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Janzophion saxis</i>	0	0	1	0	1	1	0	0	0	0	1	1	0	0	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Laticoleus infumatus</i>	0	0	2	0	1	2	0	0	0	1	1	1	0	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Laticoleus longicornis</i>	0	0	2	0	0	2	0	0	0	1	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Laticoleus palpalis</i>	-	0	2	0	0	2	0	0	0	0	1	1	?	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Laticoleus unicolor</i>	0	0	2	0	1	1	0	0	0	0	1	1	0	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Lepiscelus distans</i>	-	0	1	0	1	2	0	1	0	0	1	1	0	?	1	?	0	0	0	0	0	0	0	0	0	1	
<i>Leptophion alleni</i>	0	0	1	0	1	2	0	0	0	0	1	1	1	?	?	?	?	0	0	0	0	0	0	0	0	1	
<i>Leptophion antennatus</i>	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	



## Annex I

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

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### ORIGINAL ARTICLE

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

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### 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; Rouse & van Noort 2014; Schwarzfeld & Sperling 2014; Shimizu & Watanabe 2015a; Rouse *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)

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## Annex II

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

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## Article

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

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#### 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 *Trophophion*, 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).