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A molecular phylogeny of the parasitoid wasp subfamily Rogadinae (Ichneumonoidea: Braconidae) with descriptions of three new genera

DONALD L. J. QUICKE[1], ERINN P. FAGAN-JEFFRIES[2], JOVANA M. JASSO-MARTÍNEZ[3], ALEJANDRO ZALDÍVAR-RIVERÓN[3], MARK R. SHAW[4], DANIEL H. JANZEN[5], WINNIE HALLWACHS[5], M. ALEX SMITH[6], PAUL D. N. HEBERT[6,7], JAN HRCEK[8], SCOTT MILLER[9], MICHAEL J. SHARKEY[10], SCOTT R. SHAW[11] and BUNTIKA A. BUTCHER[1]

[1]Integrative Ecology Laboratory, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand, [2]Australian Centre for Evolutionary Biology and Biodiversity, School of Biological Sciences, The University of Adelaide, Adelaide, SA, Australia, [3]Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autonoma de México, Mexico City, Mexico, [4]National Museums of Scotland, Edinburgh, Scotland, U.K., [5]Department of Biology, University of Pennsylvania, Philadelphia, PA, U.S.A., [6]Department of Integrative Biology, University of Guelph, Guelph, ON, Canada, [7]Centre for Biodiversity Genomics, Biodiversity Institute of Ontario, University of Guelph, Guelph, ON, Canada, [8]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic, [9]National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A., [10]The Hymenoptera Institute, Redlands, CA, U.S.A. and [11]Department of Ecosystem Science, University of Wyoming, Laramie, WY, U.S.A.

Abstract. A molecular phylogeny of the subfamily Rogadinae is presented for 469 species in 52 genera representing all tribes and subtribes. The data comprise cytochrome *c* oxidase I sequences (DNA barcodes), together with a broad representation of 28S rDNA D2-D3 expansion region, EF1-**α** gene and 16S rDNA fragments. To test monophyly, most genera were represented by multiple species. The analysis of the complete dataset recovered a monophyletic Rogadinae with low support. All six tribes were recovered as monophyletic with the following relationships: (Rogadini, (Stiropiini, (Clinocentrini, (Betylobraconini, [Yeliconini, Aleiodini])))). Three new genera are recognized: *Afrorogas* Quicke **gen.n.** (type species *Afrorogas copelandi* Quicke **sp.n.**) for a mainland Afrotropical species; *Amanirogas* Quicke **gen.n.** (type species *Amanirogas isolatus* Quicke **sp.n.**), previously treated as a *Rogas* species from Tanzania; and *Papuarogas* Quicke **gen.n.** (type species *P. dameni* Quicke **sp.n.**), for species from Papua New Guinea. *Iporhogas* Granger is synonymized with *Troporhogas* Cameron. The African genera *Myoporhogas* Brues, *Scoporogas* van Achterberg and the endemic New Zealand genus *Rhinoprotoma* van Achterberg are synonymized with *Aleiodes*. A formal diagnosis of the Aleiodini Muesebeck is provided for the first time.

This published work has been registered on ZooBank, http://zoobank.org/urn:lsid:urn:lsid:zoobank.org:pub:F24DC64C-54B7-45DA-AB8E-52DC3E34545C

Introduction

The subfamily Rogadinae (Hymenoptera: Braconidae) comprises a cosmopolitan, highly species-rich group of wasps that are exclusively koinobiont endoparasitoids of Lepidoptera

Correspondence: Buntika A. Butcher, Integrative Ecology Laboratory, Department of Biology, Faculty of Science, Chulalongkorn University, Phayathai Road, Pathumwan, Bangkok BKK 10330, Thailand. E-mail: buntika.a@chula.ac.th

larvae (i.e. there is recovery from envenomation and subsequent growth and development of the host after oviposition) (Shaw, 1983; Shaw & Huddleston, 1991; Shaw, 1997a). The subfamily is divided into six tribes: Aleiodini, Betylobraconini, Clinocentrini, Rogadini, Stiropiini and Yeliconini (Zaldívar-Riverón *et al.*, 2008; Butcher & Quicke, 2015a). Rogadini have been further divided into two subtribes: Rogadina and Spinariina (van Achterberg, 1988; Zaldívar-Riverón *et al.*, 2004), although the latter was afforded tribal status by van Achterberg (1991). Species richness in the subfamily is dominated by the highly species-rich and widely distributed genus *Aleiodes* Wesmael (van Achterberg, 1995; Chen & He, 1997; Shaw, 1997b), followed by *Triraphis* Ruthe, which is relatively more species-rich in the New World lowland tropics. Both of these genera include large numbers of undescribed species (Sharkey *et al.*, 2021).

The circumscription of the subfamily has varied greatly over the years and until relatively recently has often been taken to include various subfamilies that are now recognized as distinct. Rhysipolinae, whose biology (koinobiont ectoparasitoidism – Shaw, 1983; Shaw & Sims, 2015) has been suggested as representing an intermediate stage between idiobiont ectoparasitoidism and the koinobiont endoparasitism of Rogadinae sensu stricto (Shaw, 1983), were once treated as Rogadinae in the narrow sense (e.g. Shaw & Huddleston, 1991). However, molecular phylogenetic studies have shown that they are not closely related to Rogadinae (Zaldívar-Riverón *et al.*, 2006; Sharanowski *et al.*, 2011; Quicke, 2015). Lysitermini, which are now placed as a tribe of Hormiinae (see Jasso-Martínez *et al.*, 2021) rather than as a separate subfamily (van Achterberg, 1995), were similarly treated as Rogadinae by van Achterberg (1991). Fifty-four genera of Rogadinae are currently recognized, the great majority (43) from the Old World and 19 from the New World including nine that are cosmopolitan. The principally tropical generic diversity had been rather poorly studied until van Achterberg (1991), Chen & He (1997) and Shaw (1997b) revised the Afrotropical, Chinese and New World genera, respectively. These works collectively described six new genera and provided a useful genus-level framework, which led to further studies recognizing several more new genera (Chen *et al.*, 2004; Braet & van Achterberg, 2011; Quicke & Butcher, 2011, 2015; Quicke *et al.*, 2012a, 2014; Butcher & Quicke, 2015a, Sharkey *et al.*, 2021), new species (Butcher & Quicke, 2011; Quicke et al. 2012b; Butcher *et al.* 2014; Long, 2014; Butcher & Quicke, 2015b; Sharkey *et al.* 2021) and new host records (Shaw, 2002; Maetô & Arakaki, 2005; Quicke & Shaw, 2005a,b; Quicke *et al.* 2012a, 2012b, 2012c; Sharkey *et al.* 2021). However, no comprehensive work on the Indo-Australasian genera has been conducted and the number of described Indo-Australasian taxa is almost certainly a gross underestimate of their real numbers. In addition to new taxa, several genera have been synonymized, almost all involving the recognition that named, morphologically divergent groups rendered the genus *Aleiodes* paraphyletic (see Shimbori *et al.* 2016). Additional synonyms of genera with *Aleiodes* are presented below.

With molecular data becoming increasingly available, there is a clearer picture of relationships among cyclostome braconid wasps in general (Zaldívar-Riverón *et al.*, 2006, 2008; Sharanowski *et al.*, 2011; Quicke *et al.* 2014, 2016, 2020). These studies were nevertheless limited in the number of taxa they included owing to a combination of sequencing costs, funding and availability of specimens. New research initiatives in DNA barcoding have increased the availability of data and are revealing hitherto unknown relationships (e.g. Erpenbeck *et al.*, 2012; Ramirez & Galetti, 2015; Kelnarova *et al.* 2019). Although the fast evolutionary rate displayed by the barcode region of cytochrome *c* oxidase subunit I (COI) can constrain its utility for phylogenetic studies, this may be overcome to some extent by dense taxon sampling (Quicke *et al.* 2012d). Additional support for deeper phylogenetic nodes can then be achieved by adding data from more slowly evolving gene regions as a backbone. For parasitoid wasps and other Hymenoptera, the nuclear 28S rDNA D2-D3 expansion region has become popular as an additional marker (Mardulyn & Whitfield, 1999; Dowton & Austin, 2001; Banks & Whitfield, 2006; Laurenne *et al.*, 2006; Murphy *et al.*, 2008; Ács *et al.*, 2010), with some studies also using other genes such as mitochondrial 16S rDNA and nuclear elongation factor 1−α. These gene fragments provide complementary levels of phylogenetic resolution (Klopfstein *et al.*, 2010; Trunz *et al.* 2016), which we make use of here. Most recently, because of a number of new approaches involving sequencing, many more conserved genes are starting to be applied. These include ultra-conserved elements (UCEs – Faircloth *et al.* 2012, Zhang *et al.* 2019) and anchored hybrid enrichment (Lemmon *et al.* 2012).

The first formal molecular phylogenetic study of Rogadinae was carried out by Chen *et al.* (2003), which included 20 species (11 belonging to *Aleiodes* in the current sense) and was based only on the D2 region of the 28S gene aligned using a combination of Clustal X and manual adjustment. They consistently recovered *Aleiodes* (including *Arcaleiodes* Chen & He), Clinocentrini, Rogadini (including *Spinaria* Brullé) and Yeliconini as being monophyletic, but relationships among these taxa were not strongly supported and depended on the choice of the outgroup. This was followed by Zaldívar-Riverón *et al.* (2008) with a phylogenetic study using both 28S and COI to examine the representatives of 33 genera. As with Chen *et al.* (2003), they found that *Aleiodes* and some related genera formed a clade separate from Rogadini, the tribe in which they had been previously classified. Zaldívar-Riverón *et al.* (2008) resurrected *Heterogamus* Wesmael as a well-separated sister group to *Aleiodes* based on molecular evidence even though there is apparent morphological convergence in some species of *Aleiodes*, making the separation of the two more challenging. Their analyses suggested the following tribe-level relationships: Betylobraconinae ((Aleiodini, Yeliconini), (Clinocentrini (Stiropiini, Rogadini))) (Fig. 1A).

A few subsequent studies, some focused on other subfamilies but including a reasonable representation of rogadine tribes, were all based on the same concatenation of COI and 28S gene fragments. Quicke *et al.* (2014) and Butcher *et al.* (2014) both recovered a close relationship between Aleiodini and Yeliconini

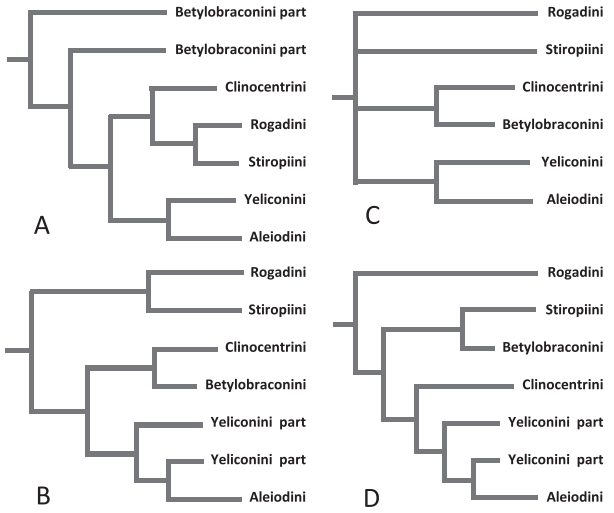

Fig. 1. Summary of tribe-level relationships from the current study and four previous investigations with taxa rendering Rogadinae paraphyletic omitted. (A) Zaldívar-Riverón *et al.* (2008); (B) Quicke *et al.* (2014); (C) Butcher *et al.* (2014). (D) Jasso-Martínez *et al.* (2021).

and also a sister group relationship between Betylobraconini and Clinocentrini (Fig. 1B, C).

Most recently, Jasso-Martínez *et al.* (2021) employed UCEs to explore rogadine relationships. Based on 411 loci from 20 nominal rogadine genera and with a wide range of outgroups, they, for the first time, recovered a robustly supported Rogadinae, inclusive of Betylobraconini. In their phylogeny, Rogadinae was the sister group to Hormiinae (inclusive of Lysitermini). Furthermore, five of the six tribes were supported as monophyletic with the following relationships: Rogadinae ((Betylobraconini, Stiropiini) (Clinocentrini (Facitorina (Yeliconina, Aleiodini))) (Fig. 1D). However, Yeliconini in the sense of Belokobylskij *et al.* (2008) (i.e. comprising the subtribes Yeliconina and Facitorina) formed a paraphyletic grade with *Yelicones* Cameron being more closely related to Aleiodini than Facitorina (represented by *Conobregma* van Achterberg and *Facitorus* van Achterberg). However, Jasso-Martínez *et al.* (2021) employed limited taxon sampling, preventing them from making additional confirmations and rearrangements in the classification in Rogadinae at tribal and genus level.

In this study, we have gathered DNA sequence data from four gene markers to assess phylogenetic relationships in Rogadinae and related subfamilies. For this, we have compiled the most comprehensive taxon sampling for the subfamily at both genus and species levels (51 genera; 346 spp.). We make use of the extensive data from DNA barcoding projects supplemented with other gene fragments with slower evolutionary rates. Our results support the monophyly of each of the six recognized tribes and various groupings within them. This sampling also helped recover the phylogenetic affinities of several enigmatic genera that had not been previously examined, leading us to propose various taxonomic updates, including the description of three new genera from the Afrotropical and Oriental regions.

Materials and methods

Taxon sampling

Taxa examined, their provenance, voucher codes and GenBank accession numbers are listed in Table S1. Our sequence data represent 50 (*ca.* 94%) of the 53 genera of Rogadinae (allowing for descriptions and synonymizations introduced here). These are distributed among the currently recognized tribes as follows: Aleiodini (2 nominal genera; 88 spp), Betylobraconini (4 genera, 17 spp.), Clinocentrini (5 genera, 56 spp.), Rogadini [32 genera (including three described here), 224 spp.], Stiropiini (3 genera, 40 spp.) and Yeliconini (6 genera, 44 spp.). Our data lack the representatives of *Aspidorogas* van Achterberg, *Cratodactyla* Szépligeti, *Cyranorogas* Butcher & Quicke, *Korupia* van Achterberg, *Pararhyssalus* Cameron, *Pegarthrum* Cameron, *Pseudogyroneuron* Baker and *Spinariella* Szépligeti. Of these, *Pegarthrum* is probably a synonym of *Macrostomion* Szépligeti (C. van Achterberg, pers comm.) and *Pseudogyroneuron* seems likely based on the broken-type specimen to be a synonym of *Aleiodes* (based on information *in litt*. C. van Achterberg). Recently, the closely related Afrotropical genera *Bequartia* Fahringer (not sequenced) and *Xenolobus* Cameron were synonymized with *Aleiodes*, and *Promesocentrus* van Achterberg with *Pilichremylus* Belokobylskij by Jasso-Martínez *et al.* (2021).

Our selection of species from the hyper-diverse genus *Aleiodes* comprised a diverse set of 64 species. Where possible, we included representatives from suggested species groups and previously synonymized genera, including all recognized subgenera (Table S2). These included 12 of the 17 species groups/subgroups proposed by Fortier & Shaw (1999), which were based on a phylogenetic analysis involving 208 species and 73 morphological characters although we recognize that many, perhaps most, of these groups are not monophyletic (Butcher *et al.*, 2012; van Achterberg & Shaw, 2016). For example, members of the *A. dispar* (Curtis) group (van Achterberg & Penteado-Dias, 1995) belong to *Heterogamus*. Because of the lack of available materials for the molecular analysis, three small species groups as defined by Shaw (1997b) and Marsh & Shaw (2003) were not represented in our study: the *gressitti*, *procerus* and *ufei* groups.

Monophyly of Rogadinae was tested by outgroup comparison using 221 terminal taxa belonging to six cyclostome braconid subfamilies. The selection emphasized the species-poor hormiine tribes Lysitermini and Hormiini, which appear to be closely related to Rogadinae according to previous molecular (Zaldívar-Riverón *et al.*, 2006; Belokobylskij *et al.*, 2008; Quicke *et al.*, 2016; Jasso-Martínez *et al.*, 2021) and morphological phylogenetic analyses (Quicke & van Achterberg, 1990; van Achterberg, 1995). Our outgroups comprised Doryctinae (14 genera, 14 species), Exothecinae (4 genera, 12 species), Hormiinae (Hormiini) (3 genera, 30 species), Hormiinae (Lysitermini) (20 genera, 87 species), Pambolinae (2 genera, 29 species) and Rhysipolinae (6 genera, 49 species). Trees were rooted with the doryctine braconid *Heterospilus prosopidis* Vierick, 1910 (Voucher: Heterospilus_prosopidis_Jo_601_UK_ex_culture).

Several previous studies (Zalívar-Riverón *et al.*, 2008) included a taxon labelled *Anachyra* van Achterberg, which was recovered among the Clinocentrini, however, that was a result of the misidentification of a species of *Tebennotoma* Enderlein (Quicke *et al.*, 2020), and therefore, it is not included here.

Molecular data

Partial fragments of genetic markers analysed were (i) concatenated fragments of the second and third domain regions of the nuclear 28S rRNA gene (*ca*. 650 bp); (ii) COI mitochondrial DNA gene (up to 679 bp); (iii) F2 copy of the nuclear elongation factor-1α gene (copy 1) (418 bp); and (iv) IV and V regions of the mitochondrial 16S rRNA gene from H2507 to H1792′ (*ca*. 650 bp) (Wu *et al.*, 2014). The COI fragment incorporates the full-length barcode sequence (sensu Hebert *et al.*, 2003; Janzen & Hallwachs, 2016). Most sequences were newly generated during this study or in previous studies by the authors (see Table S1). Genomic DNA was extracted from alcohol-preserved specimens and from dry-mounted materials up to 15 years old. Detailed information about the DNA extraction and PCR protocols employed, primers selected and sequencing procedure of PCR products can be found in the study by Zaldívar-Riverón *et al.* (2006) and on the BOLD website. Sequences of the COI, 16S and 28S markers for 25 samples of interest (Table S3) were extracted and assembled using GENEIOUS version 10.2.6 (Kearse *et al.*, 2012) from shotgun libraries as well as genomic libraries that were primarily prepared for obtaining UCE loci. We performed by-reference assemblies using as seed the COI, 16S and 28S of close-related species that were obtained in this study by Sanger sequencing. The COI sequences of the doryctines *Rhaconotus* Ruthe sp., *Lissopsius* Marsh sp. and *Stenocorse bruchivora* (Crawford) were obtained from the assembled mitogenomes by Samacá-Sáenz *et al.* (2019). The obtained assemblies were further verified by BLAST.

Sequence alignment

Protein-coding sequence alignment was trivial as no indels were present in EF1-α and very few indels were present in COI (a single codon insert in *Macrostomion* BKK0020, single codon deletions in *Aleiodes mellificus* Quicke & Butcher, *Hormius* Nees CNIN954 and 13 species of *Yelicones* Cameron, and three codon deletions in *Rectivena* van Achterberg sp. 2). The positions of indels were determined by reference to the amino acid sequence translation. The length-variable 16S and 28S rDNA sequences were aligned according to secondary structure models (Buckley *et al.*, 2000; Gillespie *et al.*, 2005; Wu *et al.*, 2014). Confidently alignable bases of both ribosomal genes were treated as either pairing (stem regions) or unpairing (length-conserved core and loop regions) (Butcher *et al.*, 2014; Quicke *et al.*, 2016, 2019, 2020). Alignments of the full sequences and our secondary structure interpretations of 28S and 16S gene fragments are provided in Appendices S1 and S2, respectively.

Phylogenetic analyses

We performed maximum-likelihood analyses with RAXML-NG and IQTREE. For the RAXML-NG analyses, we used PARTITION FINDER 2 (Lanfear *et al.*, 2017) on the CIPRES Science Gateway (Miller *et al.*, 2010) using linked branch lengths, a greedy search (Lanfear *et al.*, 2012), PHYML (Guindon *et al.*, 2010) and the corrected Akaike information criterion, was used to select the best-fit model and partitioning scheme for each individual gene alignment, and for the concatenated four-gene alignment, as follows: COI, 16S, 28S alignments all each with one partition and the GTR + I + G model, EF1-α with two partitions [codons one and three combined (GTR + I + G), codon two (TVMEF+I + G)] and the concatenated alignment with seven partitions: COI codon 2 + 28S unpaired: GTR + I + G; COI codon 3: GTR + I + G; COI codon 1: GTR + I + G; EF1-α codon 2 + EF1-α codon 3: TVM + I + G; EF1-α codon 1: GTR + I + G; 16S paired +16S unpaired: GTR + I + G; 28S paired: VMEF+I + G. RAXML-NG (Kozlov *et al.*, 2019) was used to analyse the individual genes and concatenated alignment using the best-fit models and partitioning schemes, with default settings (using the --all command) and with both Transfer Bootstrap Expectation support metric (Lemoine *et al.*, 2018) and Felsenstein's bootstrap proportions mapped onto the best scoring tree.

The IQ-TREE analyses were performed using IQ-TREE v1.6.12 (Minh et al. 2020) for the individual gene alignments and the concatenated four-gene alignment, using MODELFINDER (Kalyaanamoorthy *et al.*, 2017) to select the best models and partitioning scheme (using the --TESTNEWMERGE command), and with 1000 Ultrafast bootstrap (UFBoot) replicates conducted (Hoang *et al.*, 2018) with the --bnni command included to reduce the risk of overestimating branch supports with UFBoot. Models were selected using the default Bayesian information criterion, as follows: COI: each codon partitioned separately, models TIM2 + F + R7, TVM + F + R7 and GTR + F + R6 suggested for codons 1, 2 and 3, respectively; 28S: one partition, GTR + F + R5; 16S: one partition, GTR + F + R5; EF1-α – each codon partitioned separately with models TIM2e + I + G4, TIM3e + R3 and TNe + R2 suggested for codons 1, 2 and 3, respectively; concatenated analysis: seven partitions: EF1-α codon 2 + EF1-α codon 3: TVMe+I + G4; EF1-α codon 1: TIM2e + I + G4; COI codon 1: GTR + F + I + G4; CO1 codon 3: GTR + F + I + G4; CO1 codon 2: GTR + F + I + G4; 16S unpaired +16S paired: GTR + F + R4; 28S unpaired +28S paired: GTR + F + R5. As the concatenated analysis rendered Rogadinae paraphyletic, a constrained analysis was run using a constraint tree built with the genera that were supported as monophyletic in the analysis of Jasso-Martínez *et al.* (2021).

Trees were visualized using FIGTREE v1.4.3 (Rambaut, 2016).

Morphological examination

Specimens were imaged using an Olympus SXZ16 microscope with automated multiple image capture at preset focal

levels using an Olympus DP72 camera, and stacks of images combined using the Cell∧D image processing system. Terminology follows van Achterberg (1988) except for wing venation, which follows Sharkey & Wharton (1997); see also fig. 2.2 in Quicke (2015) for the comparison of wing venation naming systems. Institutions housing specimens of taxa described are abbreviated as follows: CUMZ (Collection of the Insect Museum, Chulalongkorn University Museum of Natural History, Bangkok); NMK (National Museums of Kenya, Nairobi); and USNM (Smithsonian Institution, Washington DC, U.S.A.).

Results

Rogadine monophyly and relationships among tribes

While all four genes did recover Betylobraconini as monophyletic, Rogadini and Aleiodini were monophyletic in the COI, 28S and 16S trees, and Stiropiini was monophyletic in COI, 28S and EF1-α trees (16S was available for only one species). Support values [IQ tree bootstrap support, Felsenstein's bootstrap proportions and transfer bootstrap expectation (TBE) trees] for each gene are given in Figs S1–S12. Nearly all analyses of the concatenated dataset recovered each of the six tribes as monophyletic (Table 1, Fig. 2; support values are given in Figs S13–S15), the exception being Clinocentrini in the IQ tree (Fig. S13).

All tribes except Yeliconini were recovered as monophyletic in at least some of the single gene analyses. Rogadini were monophyletic in the COI analyses (Figs 2, S7–S9) and in the 28S IQ TREE (Fig. S4). Aleiodini was strongly supported as monophyletic in most analyses of COI, 16S and 28S genes (Figs 2, S1–S4, S7–S10). For 16S, we only had a single species of Stiropiini, but the tribe was monophyletic in the 28S and EF1-α IQ trees (Figs S4, S10) and in all COI analyses (Figs 2, S7–S9). Betylobraconini and Clinocentrini were not represented by many taxa in most of the single gene analyses. However, betylobraconines were monophyletic in all 16S analyses (Figs S1–S3), and, with the exception of Gondwanocentrus, in the Raxml-NG analysis of COI (Figs S8, S9). Clinocentrines were only recovered as monophyletic in the Raxml-NG analysis of 28S (Figs S5–S6). Yeliconini were not recovered as monophyletic in any single gene analysis, but there were no taxa that consistently caused this.

Relationships within Aleiodini, Betylobraconini and Clinocentrini

Two clades were recovered in all analyses: one comprising all *Heterogamus* species and the other all *Aleiodes* (Figs 3 and 4) plus the nominal genera *Myoporhogas* Brues, *Scoporogas* van Achterberg and *Rhinoprotoma* van Achterberg. Within *Heterogamus*, the New World species form a clade nested within a paraphyletic Old World group of species.

Table 1. Support values for the six Rogadinae tribes in the three concatenated analyses.

Taxon	IQTREE 2	RAXML-NG: FBP support values	RAXML-NG: TBE support values
Aleiodini	99	76	92.5
Betylobraconini	61	29	92
Clinocentrini	-	11	38
Rogadini	100	63	81
Stiropiini	100	100	99.9
Yeliconini	95	62	96.9

Betylobraconini (Fig. 5), represented by four nominal genera, received only moderate support. The Chilean genus *Gondwanocentrus* Quicke & Butcher was recovered as the sister group of the Australasian species. Both *Betylobracon* Tobias (represented by the type species) and *Pilichremylus* were recovered nested among the 13 representative *Mesocentrus* Szépligeti species.

Clinocentrini were represented by all five known genera: *Artocella* van Achterberg, *Clinocentrus* Haliday, *Confusocentrus* Quicke & Butcher, *Kerevata* Belokobylskij and *Tebennotoma*. However, support for this tribe (Fig. 6) was the lowest of all in each case (Table 1). The Western European genus *Artocella* was weakly supported as the sister group to the remaining taxa. *Clinocentrus* was recovered as paraphyletic with respect to the three other genera, each of which formed a monophyletic cluster. The Australasian genera *Kerevata* and *Confusocentrus* were sister groups and the larger of the *Clinocentrus* clades, while the OW genus *Tebennotoma* was moderately well supported as the sister group to two Neotropical members of *Clinocentrus*. Careful examination of the voucher specimens of the two isolated Neotropical *Clinocentrus* species shows them to have the metasomal tergites beyond the middle of the tergum 2 weakly sclerotized and unsculptured, but they agree well with *Clinocentrus*, so we refrain from making taxonomic changes for these. Similarly, *Confusocentrus* and *Kerevata* were recovered within *Clinocentrus* but with various relationships in both 28S and COI individual analysis, and given that Clinocentrini were not well represented in the dataset and received weak or no support, we refrain from synonymizing them here.

Relationships within Rogadini

Rogadini were recovered as monophyletic with moderate to strong support in all concatenated analyses (Table 1, Figs 6 and 7). Several well-supported genera and genus groups were apparent. The previously recognized *Colastomion* Baker group of genera (Quicke *et al.*, 2012c; Ranjith *et al.*, 2018; Sharkey *et al.* 2021) (i.e. *Bioalfa* Sharkey, *Colastomion*, *Cystomastacoides* van Achterberg, *Cystomastax* Szépligeti, *Hermosomastax* Quicke, *Macrostomion*, *Megarhogas* Szépligeti and *Myocron* van Achterberg) were recovered as monophyletic (Fig. 6). None of the nominal *Colastomion* group of genera were recovered as monophyletic with the exception of

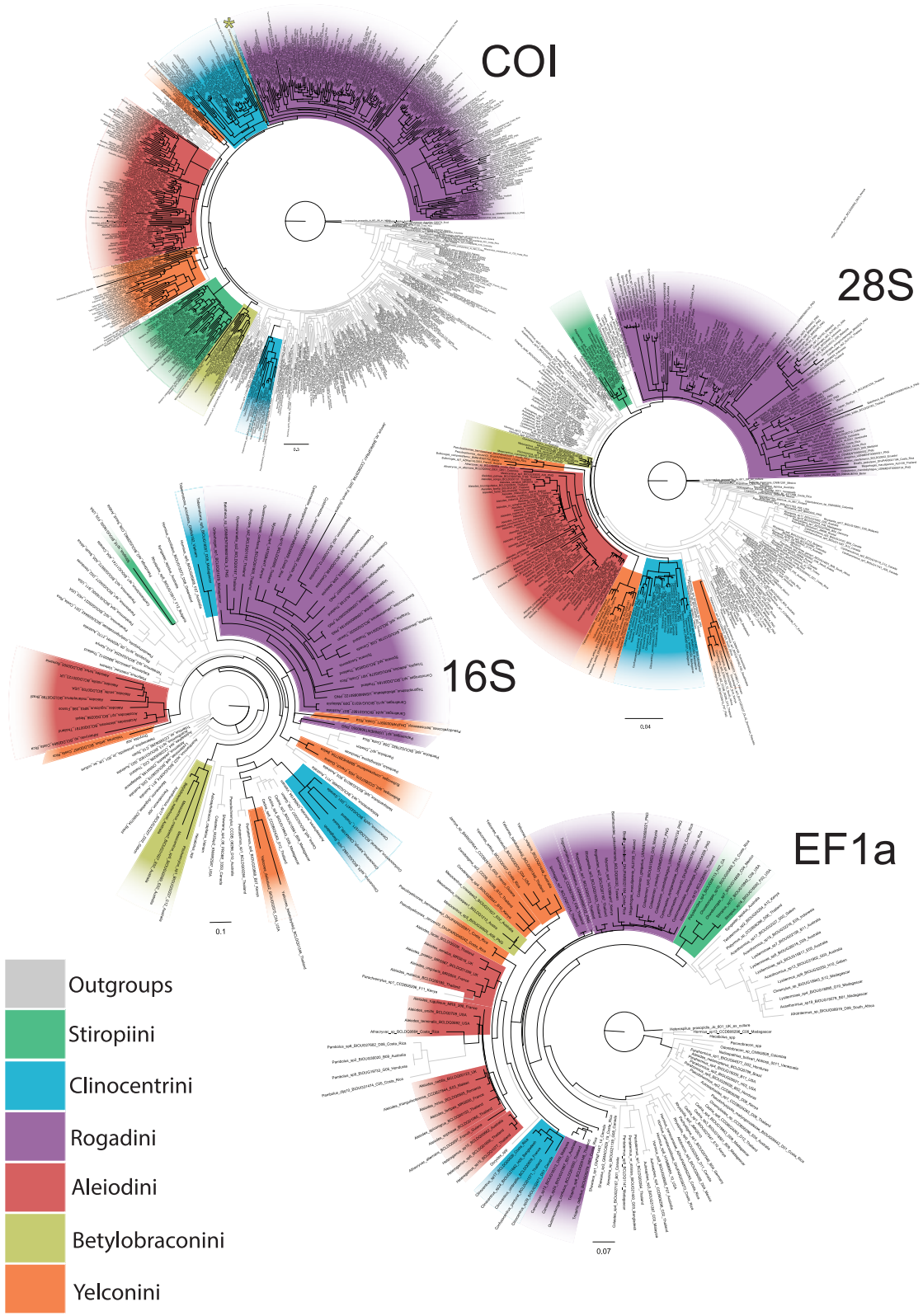

Fig. 2. RAXML-NG maximum-likelihood phylogenies for each of the separate gene fragments analysed separately with all terminals shown and major groups indicated.

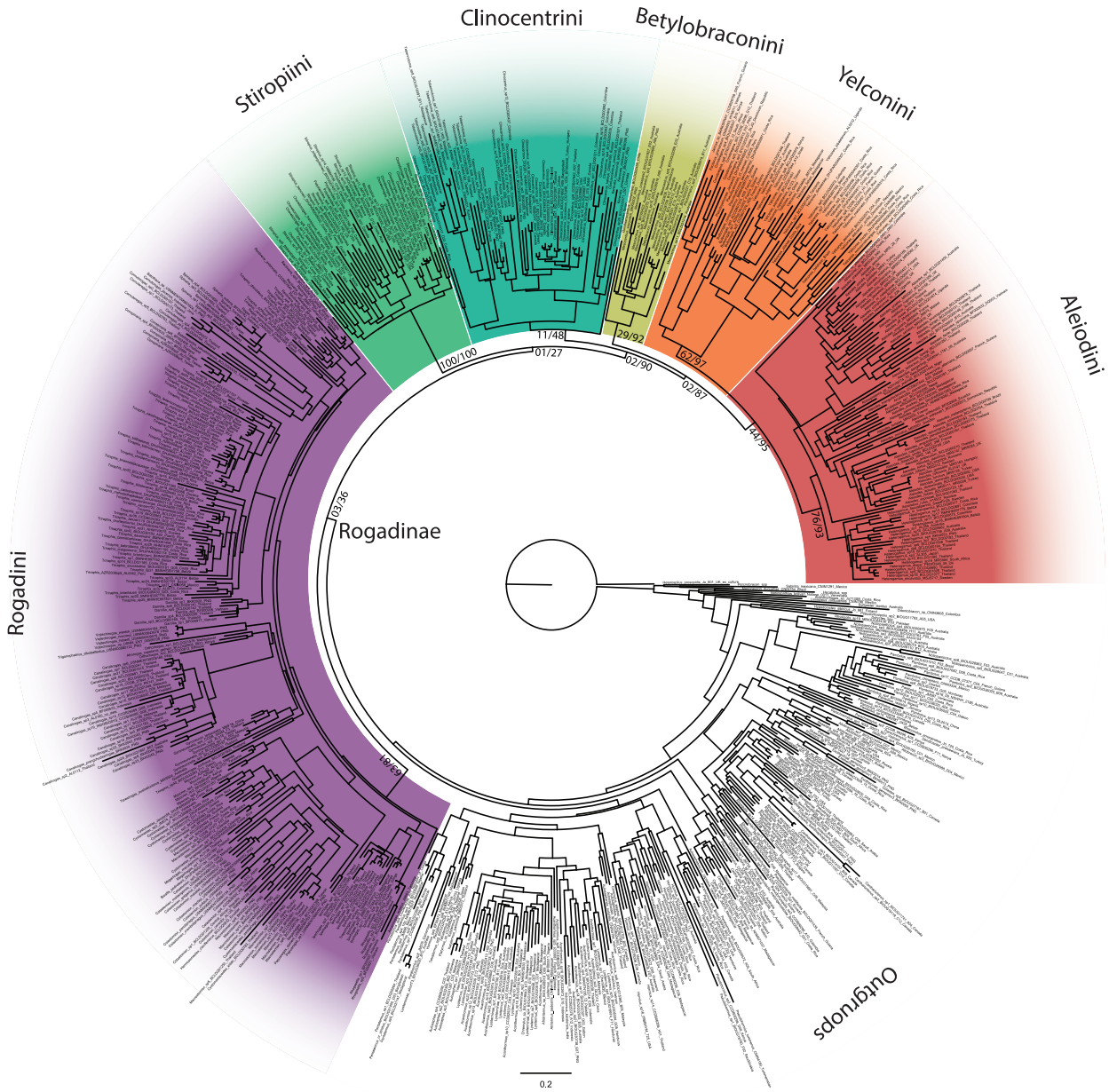

Fig. 3. RAXML-NG maximum-likelihood phylogeny of Rogadinae sequences with all terminals shown and major groups indicated. Support values for major clades are ML Felsenstein's bootstrap proportion (on left) and transfer bootstrap expectation (on right).

the Afrotropical *Myocron*, which formed a sister group to the remaining taxa. The Old World species assigned to *Macrostomion* were recovered together with *Cystomastacoides* and one species of *Colastomion*, and formed two well-supported clades. The three Neotropical species identified as *Macrostomion* were recovered as a strongly supported clade nested within the Neotropical genus *Cystomastax* (Fig. 7), far removed from apparent Old World congeners. Further investigation will be required to determine whether one of the two groups represents a separate genus. The recently described Neotropical genera *Bioalfa* and *Hermosomastax* were each recovered as sister groups to Old World clades. The Old World genera *Canalirogas* van Achterberg & Chen (S.E. Asia to Australia), *Orthorhogas* Granger (Africa) and *Vojtechirogas* Quicke (Papua New Guinea) formed a well-supported clade close to the *Gyroneuron* Kokujev and *Gyroneuronella* Baker.

The subtribe Spinariina van Achterberg, comprising *Batotheca* Enderlein, *Batothecoides* Watanabe, *Conspinaria* Schulz, *Cornutorogas* Chen, Belokobylskij, van Achterberg & Whitfield, *Spinaria* Brullé and *Spinariella* (not sampled

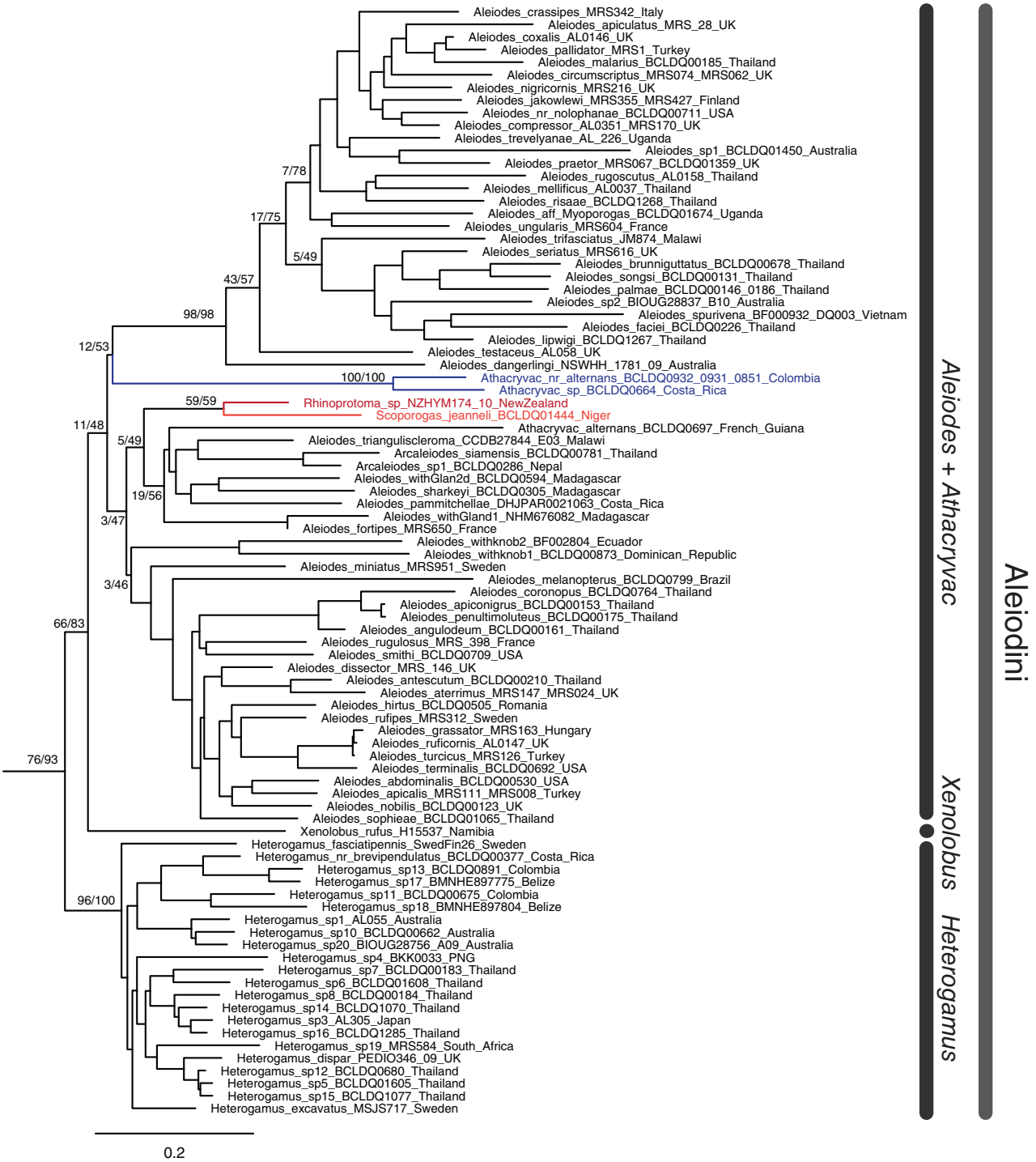

Fig. 4. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within for Aleiodini. Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

here), was recovered as a sister group to *Rogas* sensu stricto, both groups being entirely from the Old World (Fig. 8). Together with *Darnilia* van Achterberg, these rendered the cosmopolitan genus *Triraphis* polyphyletic. *Triraphis* is almost perfectly divided into New and Old World clades except that two species from Costa Rica and North America [i.e. *T. discoideus* (Cresson)] are nested among the Old World ones, which include the type species [*T. tricolor* (Wesmael)] (Fig. 8). The separation of the two largely geographic clusters was also apparent in the single gene 28S (Figs S4–S6) and COI

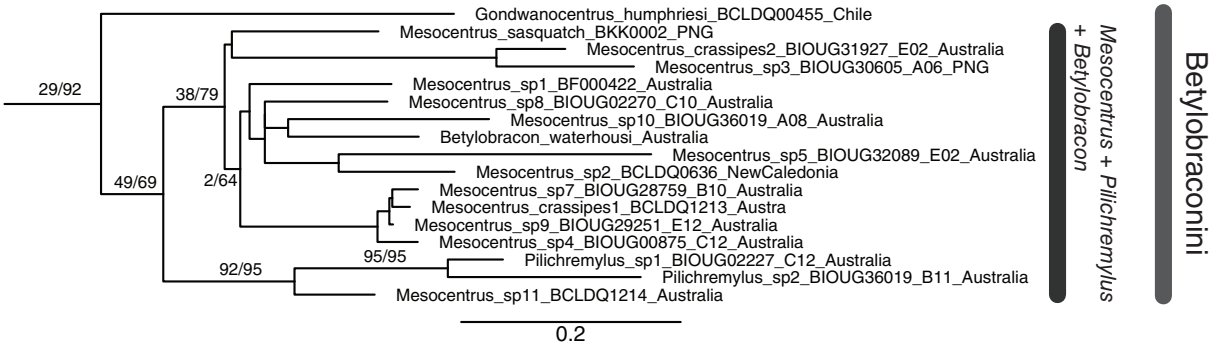

Fig. 5. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within Betylobraconini. Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

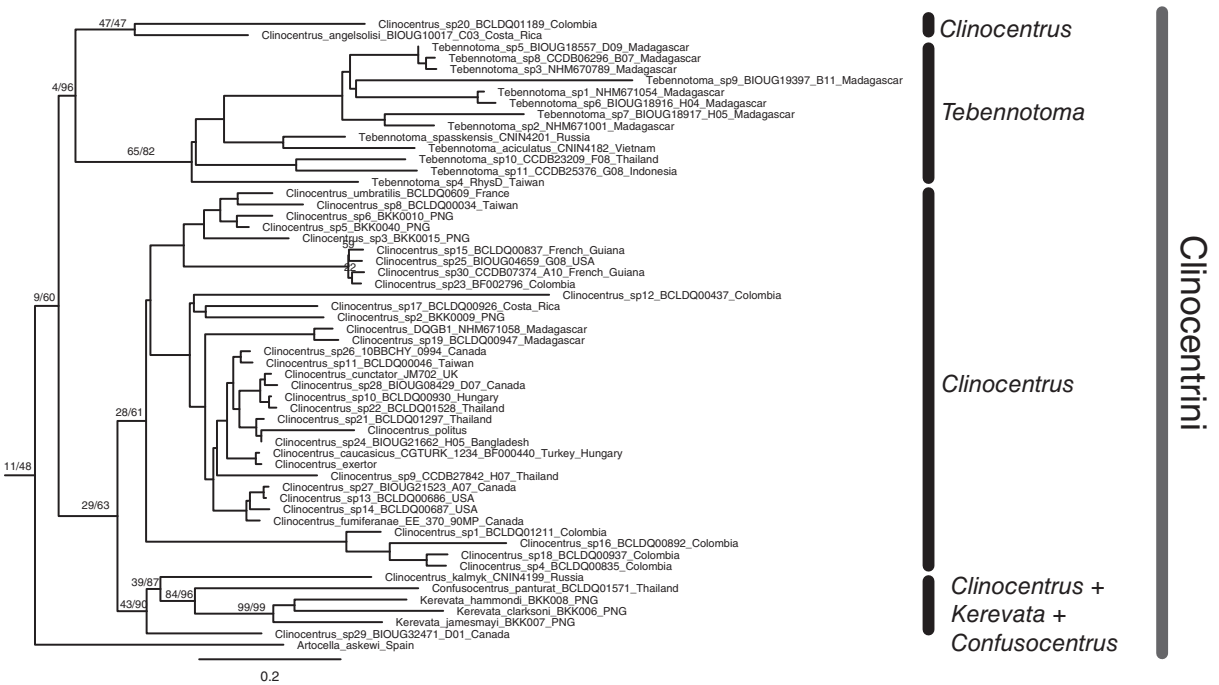

Fig. 6. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within Clinocentrini. Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

(Figs S7–S9) analyses and the four-gene IQ analysis (Fig. S13); too few species were represented by the other genes to draw conclusions. One isolated species of *Triraphis* from Gabon (Triraphis_sp40_BIOUG32283_F11_Gabon) was far removed from the others and was instead placed closest to *Quasimodorogas* Quicke & Butcher in combined analyses and well removed from other *Triraphis* in all separate COI and 28S analyses. Re-examination of the voucher confirmed that morphologically, it appears to have been correctly identifed.

Relationships within Stiropiini

The entirely New World tribe Stiropiini (Fig. 9) was strongly supported as monophyletic in all analyses. The sampled material includes several species not as yet identified to genus. However, of the specimens that could be identified, members of the three genera are not clearly separated and support values of branches within the tribe are rather low.

Relationships within Yeliconini

In the RAXML-NG analyses of the concatenated datasets, Yeliconini was strongly supported as monophyletic (97 TBE) (Figs 10, S13–S15), as was each of the included genera represented by multiple species, i.e. *Yelicones* (99 TBE), *Pseudoyelicones* van Achterberg, Penteado-Dias & Quicke (100 TBE) and *Bulborogas* van Achterberg (100 TBE). In addition, the subtribe Facitorina was also recovered as monophyletic (99

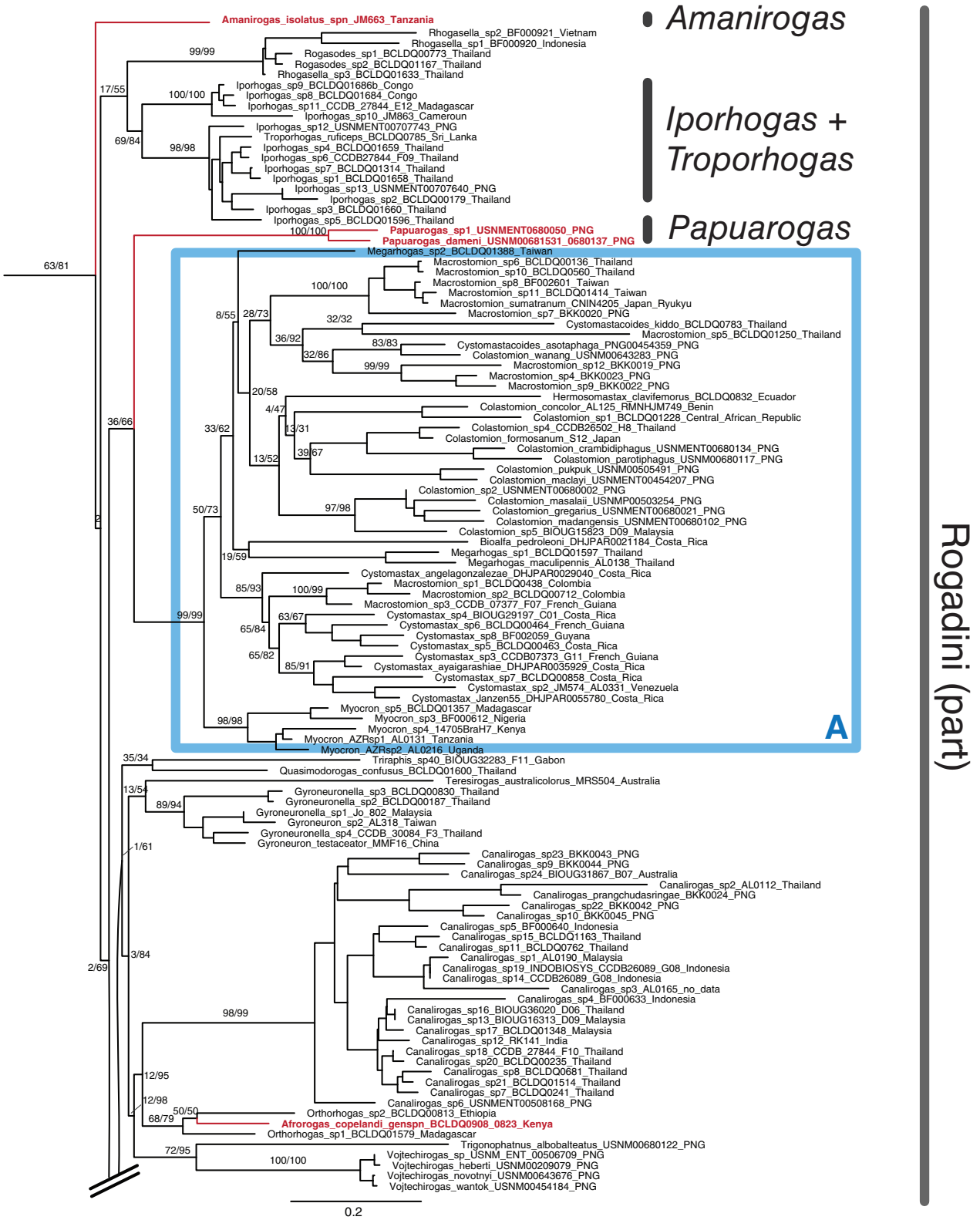

Fig. 7. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within basal part of Rogadini clade (including *Cystomastax* group indicated in blue box 'B') and the two new genera indicated in red. The tree is contiguous with Fig. 7. Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

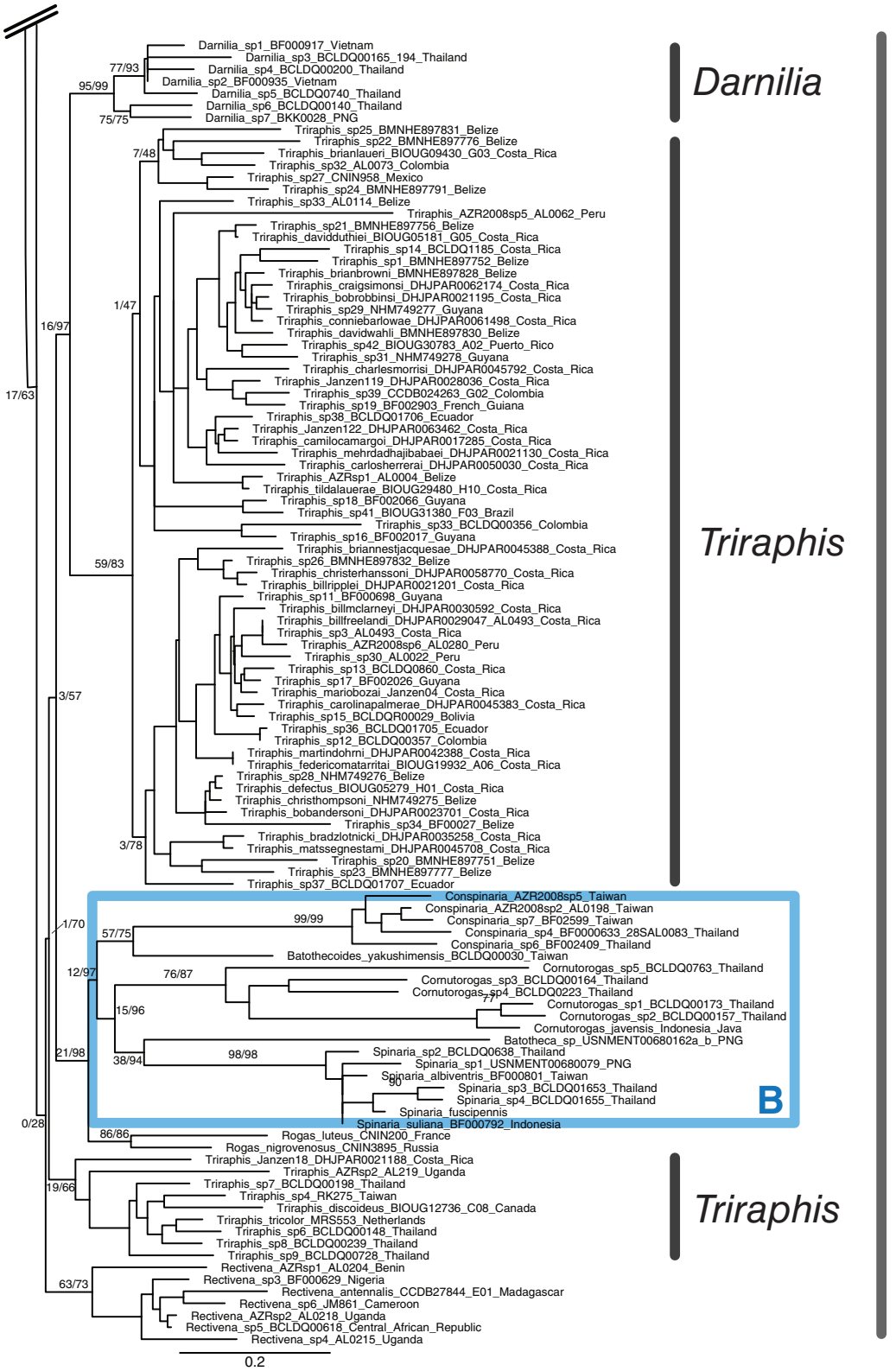

Fig. 8. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within remainder of Rogadini clade (including 'Spinariina' indicated in blue box 'B'). Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

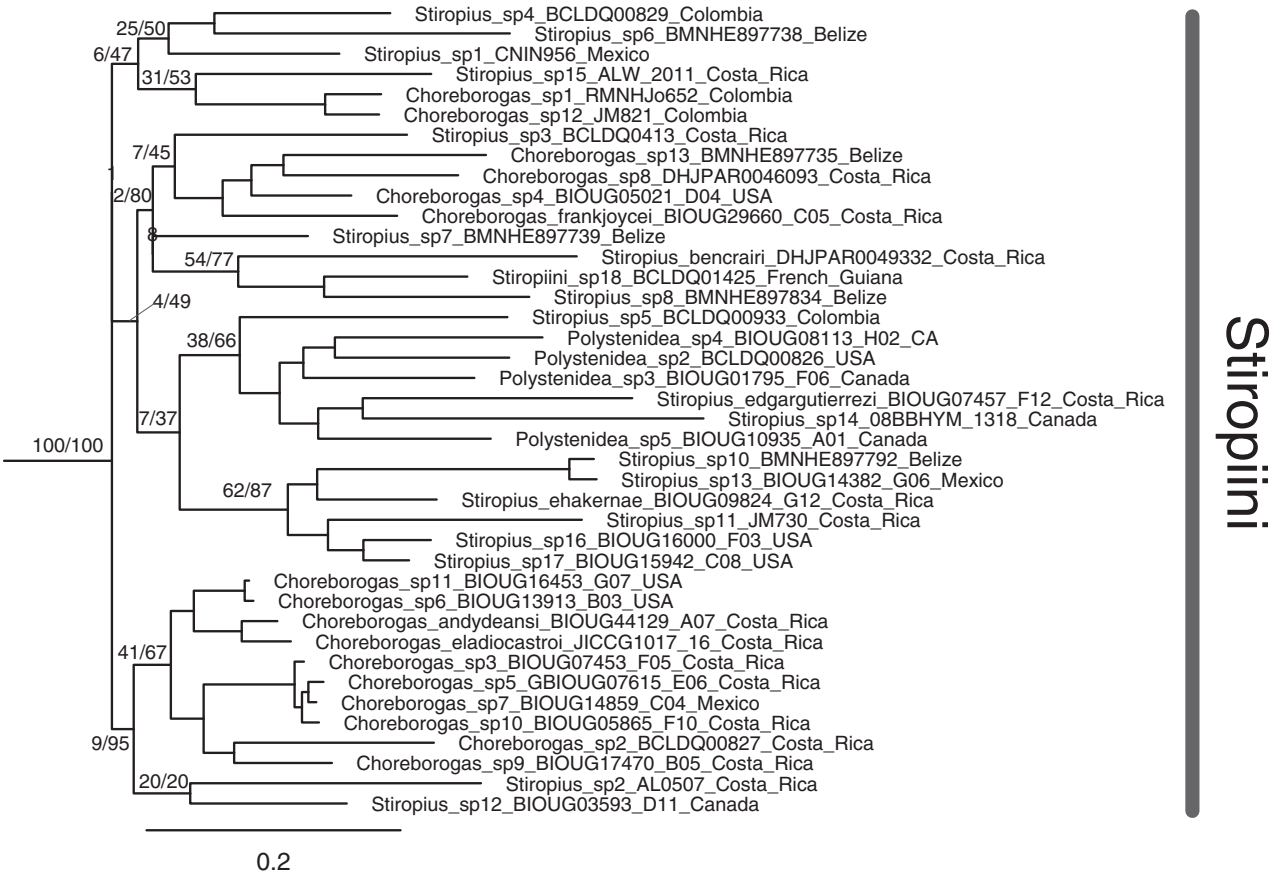

Fig. 9. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within Stiropiini. Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

TBE) but of its included genera, *Facitorus* and *Jannya* van Achterberg were both nested with a paraphyletic *Conobregma*, though with weak support.

Discussion

Monophyly and tribal relationships of Rogadinae

The past concept of Rogadinae has been far broader and often has included Hormiinae and Lysiterminae (Quicke, 2015). However, over the past 20 years, virtually all workers have applied a narrower definition largely based on their koinobiont endoparasitism and mummification of the host larva, although this is still unknown for Betylobraconini (Shaw, 1997b). Hormiines in contrast display a presumed plesiomorphic idiobiont ectoparasitoid biology. Monophyly of Rogadinae is supported by our combined data and is also indicated by the almost ubiquitous presence of two morphological features: a mid-longitudinal carina on the second metasomal tergite and the widespread presence of a comb of setiform processes within the secondary venom duct (Zaldívar-Riverón *et al.*, 2004). Previous molecular phylogenetic studies based on Sanger sequence data including multiple representatives of presumed Rogadinae, Lysiterminae, Hormiinae and some members of Cedriina (i.e. *Cedria* Wilkinson and *Carinitermus* van Achterberg, and *Aulosaphobracon* Belokobylskij & Long) have all rendered Rogadinae paraphyletic (Quicke *et al.*, 2014; Ranjith *et al.*, 2017). Here, a considerably expanded taxon and gene sampling recovered Rogadinae (including Betylobraconinae) as monophyletic for the first time (Fig. 3). This is concordant with a recent UCE study by Jasso-Martínez *et al.* (2021) (with 100% support based on 411 UCE loci). However, in contrast to our best estimate, the study by Jasso-Martínez *et al.* (2021) intermingled the subtribes of Lysitermini with Hormiini with strong support, so they united their members under Hormiinae. In our combined analyses, NG tree (Fig. 3), a group around *Cedria*, was placed basally and the enigmatic *Aulosaphobracon* as sister to the nearly perfectly separated Lysitermina s.l. (including *Pentatermus* Hedqvist and *Tetratermus* Wharton) and Hormiina. Based on these results and those of Jasso-Martínez *et al.* (2021), we conclude that Hormiinae (inclusive of Lystitermini) and Rogadinae underwent a rapid radiation as suggested by the predominantly short internal branches (Whitfield & Kjer, 2008), leaving relatively little phylogenetic signal, even when compared using genomic data. Moreover, the transition to endoparasitoidism (with host

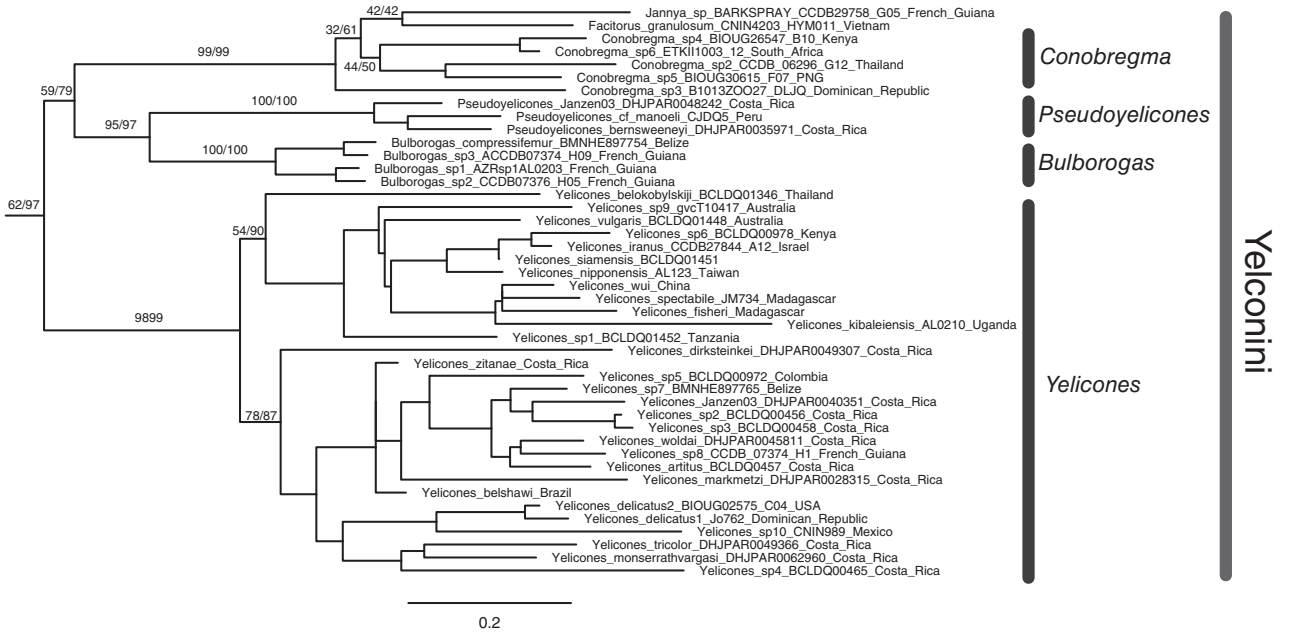

Fig. 10. Subtree from the four-gene concatenated RAXML-NG maximum-likelihood phylogeny showing recovered relationships within Yeliconini. Support values are presented as Felsenstein's bootstrap proportions/transfer bootstrap expectation.

mummification) likely occurred only once. Unlike most koinobiont endoparasitoid ichneumonoids, the eggs of Rogadinae are relatively large, more similar to those of synovigenic idiobionts. It is possible, therefore, that this reflects a close relationship with their idiobiont sister group Hormiinae.

Our best tree (Fig. 3) displays the tribe-level relationship Rogadini (Stiropiini (Clinocentrini (Betylobraconini (Yeliconini (Aleiodini))))), in contrast to previous studies (see Fig. 1). The low signal again may reflect the rapid divergence of several tribes. All recent molecular studies have agreed, however, that Rogadini are sister to the rest of the group (Fig. 1B–D) despite their apparently more specialized biology compared with Clinocentrini (Shaw, 1983). All studies also agree on a close relationship (sister group or grade) between Aleiodini and Yeliconini (e.g. Zaldívar-Riverón *et al.*, 2008; Quicke *et al.*, 2014). This is supported by the characteristic found in at least *Yelicones* and *Pseudoyelicones*, which produce hard, strongly tanned host mummies, usually with emergence of the adult parasitoid from the mummy's posterodorsal part (Zaldívar-Riverón *et al.*, 2008; Quicke *et al.*, 2018). A tendency towards the evolution of a similar morphology with strongly thickened femora and shortened tarsi is also found within *Aleiodes* itself, for example in the Thai species *A. globifemurus* Quicke & Butcher, *A. nonicones* Quicke & Butcher and *A. pseudicones* Quicke & Butcher (Butcher *et al.*, 2012), and in the New Zealand *Rhinoprotoma* (see below) (van Achterberg, 1995).

The phylogenetic position of *Aulosaphobracon* has been uncertain. It was originally included within its own monogeneric tribe in Betylobraconinae (sensu Belokobylskij & Long, 2005). Its relationship to other groups has not been conclusively resolved in several recent molecular phylogenetic analyses based on just a few gene fragments (e.g. Zaldívar-Riverón *et al.*, 2008; Quicke & Butcher, 2015; Quicke *et al.*, 2016) although it has usually been recovered associated with hormiine taxa or more basally weakly supported as the sister to Rogadinae+Hormiinae. In the UCEs study by Jasso-Martínez *et al.* (2021), it was recovered with Hormiinae, similar to our findings (Fig. 3).

Relationships within tribes

Our analyses strongly support the tribal-level placement of Betylobraconini (formerly Betylobraconinae) within Rogadinae as previously proposed by Butcher & Quicke (2015a) as it is recovered as monophyletic in the analysis with all taxa (Fig. 1) and separate from all other ingroup taxa in the Rogadinae-only analysis (Fig. 2).

Heterogamus represents the sister to *Aleiodes* including the nominal genera *Athacryvac* Braet & van Achterberg, *Myoporhogas*, *Rhinoprotoma*, *Scoporogas* and *Xenolobus*. In agreement with Shimbori *et al.*'s (2016) conclusions based upon morphology, we recovered *Athacryvac* within *Aleiodes*, though quite basally (Fig. 4). *Arcaleiodes* was synonymized with *Aleiodes* (Belokobylskij, 2000) and treated as a subgenus of *Aleiodes* (Zaldívar-Riverón *et al.*, 2008, Butcher *et al.*, 2012). The two *Arcaleiodes* species were recovered nested within a basal clade of *Aleiodes* that includes *Athacryvac*, the *Hemigyroneuron* Baker group of species and several species of *Aleiodes* that have traditionally been placed in the subgenus *Chelonorhogas* Enderlein. The males of *A. cameronii* (Dalla Torre), *A. fortipes* (Reinhard), the subgenera *Hemigyroneuron* [except *A.* (*H.*) *dubiosus* (Fullaway)], *Arcaleiodes* and some Malagasy species possess a large, paired gland in metasomal

segments 4–6 that opens into a medioposterior pore (Butcher & Quicke, 2011). Shaw *et al.* (1997) noted this character as present in the males of *A. cameronii* and several other species of the *pulchripes* species group as they defined it but that is not present in all species in that group, nor is it present in *A. dissector* (Nees) and its close relatives and *A.* (*Athacryvac*). This feature is only found in this group and may represent a synapomorphy for the clade.

The Aleiodes *'gland group' and status of subgenus* Hemigyroneuron

The subgenus *A.* (*Hemigyroneuron* Baker) has been characterized entirely on the basis of the distally expanded fore wing subbasal cell with a glabrous zone and sometimes a separate sclerome in the membrane (Quicke & Butcher, 2011). This feature has evolved independently in the *Gyroneneuron* + *Gyroneuronella* group in Rogadini, and some species of *Hemigyroneuron* show a remarkably similar modification (Butcher & Quicke, 2015b). The males of most species (when known) possess a paired metasomal gland that opens at a single subposterior or medial pores of various sizes on metasomal tergites 4–6 (Quicke & Butcher, 2011). These pores are also present in the males of several species of the *A. pulchripes* Wesmael subgroup of the *Aleiodes apicalis* grade (Shaw *et al.*, 1997; Delfín & Wharton, 2000), including the New World *A. cameroni* (Dalla Torre) and *A. pammitchellae* Sharkey (Fig. S16), the Palaearctic *A. fortipes* (Reinhard) and several undescribed *Aleiodes* species from Madagascar (*Aleiodes*_withGland1 and *Aleiodes*_withGland2 in Fig. 4). Collectively, these taxa form a close group in our trees (Fig. 4) (together with an oddly placed *A. (Athacryvac) alternans*). However, these male glands opening at a central pore are absent from *Aleiodes (Hemigyroneuron) dubiosus* (Fullaway) and from *A. (H.) dangerlingi* Quicke & Butcher (and presumably in the closely related *Aleiodes (H.) ellingsenae* Butcher & Quicke). The first of these is known only from the female-type specimen from the Philippines, but we have obtained sequence data for *A. dangerlingi*, also only known from a female, which our analyses place far from the 'gland group'. We strongly suspect that the modified fore wing venation is homoplastic and that as currently constituted, *A.* (*Hemigyroneuron*) is not monophyletic.

The large-bodied (fore wing 14–16 mm), Afrotropical *Xenolobus* (undoubted sister group to *Bequartia* Fahringer, see van Achterberg, 1991) was recovered nested within *Aleiodes* in the combined gene IQ TREE (Fig. S15) in agreement with UCE findings, but recovered as sister to *Aleiodes* in the ML tree (Figs 3, S14, S15). Features of the venom apparatus of *Xenolobus* place it in Aleiodini rather than Rogadini (Zaldívar-Riverón *et al.*, 2004). These wasps have simple claws, without an angulate basal lobe, but also possess several autapomorphies (van Achterberg, 1991), notably in the case of *Xenolobus* and *Bequartia* the fore wing vein r-rs arises more or less contiguously with the basal part of the pterostigma (see figs 1, 18 in van Achterberg, 1991), a highly modified propodeum without a midbasal longitudinal carina (but rather densely vertically setose), sublateral (presumably glandular) pits often in male *Xenolobus* and with a bisinuous transverse carina in females. It appears most likely that both *Bequartia* and *Xenolobus* are derived species groups within *Aleiodes*, but their extreme morphological divergence would seem to make recognition at subgeneric level sensible, although we refrain from doing so here because of current uncertainty about exact relationships.

Status of Scoporogas

Association of *Scoporogas* (=*Scophthalmus* Szépligeti) with *Aleiodes* rather than Rogadini was indicated by the features of the venom apparatus (Zaldívar-Riverón *et al.*, 2004). *Scoporogas* differs from *Aleiodes* only in having the hind wing vein 1RS sclerotized on the basal third and strongly curved – the other character states mentioned in van Achterberg's (1991) key to genera are all variable within *Aleiodes*; many *Aleiodes* have strongly pectinate claws and a trace of hind wing vein r-rs (arising at the apex of the curved part of 1RS) is also present in some *Aleiodes*, e.g. *A. spurivena* Quicke & Butcher. We therefore formally synonymize *Scoporogas* van Achterberg with *Aleiodes* Wesmael, **syn.n**. [hence *Aleiodes jeanneli* (*Szépligeti*) **comb.n.].**

Status of Myoporhogas

Van Achterberg (1991) retained *Myoporhogas* (=*Microrhogas* Szépligeti) separate from *Aleiodes* 'despite its similarity' on the basis of posteriorly converging fore wing veins 1-M and m-cu and its lack of a mid-anterior propodeal carina. Although the specimen examined for molecular data here was not the type species (i.e. *M. ocellaris* Szépligeti), it was sufficiently similar that we are confident that it is closely related to it. Nearly all *Aleiodes* species possess a distinct mid-longitudinal carina at least on the anterior of the propodeum, but it is secondarily lost in some species such as *A. atuin* Quicke & Butcher. We therefore formally synonymize *Myoporhogas* Brues with *Aleiodes* Wesmael, **syn.n.** [hence *Aleiodes ocellaris* (Szépligeti) **comb.n.**].

Status of Rhinoprotoma

Rhinoprotoma is known only from New Zealand. Females have a derived morphology, which led to it being placed in a separate genus by van Achterberg (1995) though males, which were not known at the time, are far less derived (Fig. S17). It differs from most *Aleiodes* in lacking a mid-longitudinal propodeal carina and any trace of a mid-basal area on the second metasomal tergite, and in having a rather protruding face and shortened tarsi. Apart from these characters, there are no obvious external morphological characters to suggest that *Rhinoprotoma* is not a derived *Aleiodes*. *Rhinoprotoma is strongly supported within Aleiodes in our concatenated analyses* (Figs S13–S15), 28S (Figs S4–S6) and in the RAXML-NG trees based on COI

(Figs S8, S9). Furthermore, its 28S sequence possesses the 28S D2 AGCGT motif characteristic of all *Aleiodes* (instead of TGCGT, which is highly conserved within Braconidae), corresponding to the 3′ base at the end of the unpaired region and following four paired bases of stem region 3 (see fig. 1 in Gillespie *et al.*, 2005). Therefore, we formally synonymize *Rhinoprotoma* van Achterberg with *Aleiodes* Wesmael (hence *Aleiodes masneri* [van Achterberg] **n.comb.**).

Rogadini

Monophyly of the tribe Rogadini was well supported in both analyses. No members of the Aleiodini, Betylobraconini, Clinocentrini, Stiropiini or Yeliconini clades possess a protruding (angular, square or rounded) basal lobe to the claws, whereas most genera of Rogadini do – notable exceptions are *Batotheca*, *Batothecoides*, *Colastomion*, *Macrostomion*, *Orthorhogas* and some species within both *Canalirogas* and *Teresirogas* Quicke & Shaw. Therefore, it seems likely that a protruding basal lobe is a synapomorphy for Rogadini but has been secondarily lost on several occasions.

Within Rogadini, only a few clades were recovered with strong support in this study, including the *Colastomion* group of genera (Figs 7, S7–S9, S11, S12), *Gyroneuron* + *Gyroneuronella* (89/94) (Fig. 8) and Spinariina+*Rogas* (21/98) (Fig. 8). With lower levels of support, though perhaps also noteworthy, are the sister groupings of *Iporhogas* Granger with *Troporhogas* Cameron (69/84; see below), *Canalirogas* with *Vojtechirogas* and *Trirhaphis* with *Darnilia*.

Recovery of *Gyroneuron* sister to *Gyroneuronella* is hardly surprising. These genera are extremely similar with highly derived fore wing venation (Butcher & Quicke, 2015b), and they probably ought to be synonymized. However, the morphological differences between them seem consistent so at present, we prefer to keep them separate. Nothing is known of their biology despite their being collected relatively frequently at light traps and in Malaise traps in S.E. Asia.

The *Colastomion-Cystomastax* group as currently recognized comprises *Bioalpha* Sharkey, *Colastomion*, *Cystomastacoides* van Achterberg, *Cystomastax* Szépligeti, *Hermosomastax* Quicke, *Macrostomion*, *Megarhogas* and *Myocron* (Quicke *et al.*, 2012c). These taxa all share a very elongate first metasomal tergite, which is narrowed subbasally, a more or less strongly convex female hypopygium (also present in *Orthorhogas* and *Afrorogas* **gen.n.**), and the hind tibial spurs being rather strongly curved and at least partially glabrous, although the last character is less evident in *Cystomastax*. *Myocron* is strongly supported as the sister group of all the other taxa in this group. However, *Macrostomion* is polyphyletic. Most notably, three New World species were strongly supported as a clade rendering *Cystomastax* (an entirely New World genus) as paraphyletic. New World representation of *Macrostomion* was documented by Shaw (1997b) although he noted that several New World records prior to his publication were based upon misidentifications. One of us (DLJQ) has previously also noted New World specimens that would fall in *Colastomion*. The remaining *Macrostomion* species (all Old World) formed several small groups nested among *Colastomion* and *Cystomastacoides*. We are surprised that New World *Cystomastax* and Old World *Cystomastacoides* are strongly supported belonging to different clades as they share pointed basal lobes to the claws and hind coxae with a dorsal protruding ridge (tubercle). However, the lobed claws are probably symplesiomorphic and the hind coxal modifications may be evolutionary adaptations for stabilizing the metasoma during oviposition. The available biological data for these are limited. Several *Colastomion* from Papua New Guinea and Japan have been reared as solitary or gregarious parasitoids of Crambidae (Quicke *et al.*, 2012b; Sakagami *et al.*, 2020), whereas all records for *Macrostomion* are as gregarious parasitoids of Sphingidae (Shaw, 2002; Maetô & Arakaki, 2005). Based on morphology alone, it would not seem unreasonable to synonymize Old World *Colastomion*, *Macrostomion* and *Megarhogas* since the characters separating them are either rather weak and likely homoplastic (*Colastomion* and *Macrostomion*) or, in the case of *Megarhogas*, only separated by one clear autapomorphy of fore wing venation (a swollen junction between fore wing veins r-rs, 3RSa and 2RS). However, the available biological data indicate that there is a clear distinction.

With the exception of one species from Gabon, the 76 included species of *Triraphis* formed two separate clades rendered paraphyletic by *Darnilia*, *Rogas* sensu stricto and Spinariina (Fig. 8). The better-represented clade comprised entirely New World species and was recovered as sister to the Old World *Darnilia* with relatively strong support. The other clade formed the sister to the large *Triraphis* + *Darnilia* + *Rogas* + Spinariina clade and comprises all the Old World species including the type species, *T. tricolor*, together with two New World species, one from North America and one from Costa Rica.

Darnilia was described by van Achterberg (1989) based on a single Indonesian species reared from the caterpillars of Limacodidae (i.e. *Darna trima* Moore and *D. sordida* Snellen). Species in this genus have since been recorded from China, Thailand and Vietnam. In the original description, van Achterberg (1989: 89) notes that "[it is] closely related to the genus *Triraphis* Ruthe stat. nov., but *Triraphis* has vein M+CU of hind wing about as long as 1-M, dorsope of first tergite distinct, vein 1-M of fore wing long, and vertex smooth". Of these, the absence of dorsope and laterope in *Darnilia* may be considered as apomorphic and appear to be consistent although some specimens do have a distinct weak dorsope.

Spinariina were recovered in a single clade along with the type species of *Rogas*. No specimens of the rare genus *Spinariella*, known only from Borneo and Sulawesi, were available for the study, but based on morphology, it almost certainly belongs in Spinariina (van Achterberg, 2007). Monophyly of *Rogas* sensu stricto with Spinariina has also been found in earlier analyses with lower taxon sampling (e.g. Quicke *et al.*, 2014). Interestingly, virtually all Rogadinae have the dorsal carinae of the first metasomal tergite united forming either a semicircular or Y-shape, but one of the diagnostic characters of *Rogas* is that the dorsal carinae remain separated. This character state is also found in Spinariina genera *Batothecoides*, *Conspinaria*,

Cornutorogas and *Spinaria* (van Achterberg, 2007), a few *Triraphis* [including the type species *T. tricolor* (Wesmael); see van Achterberg, 1991] and in some species of *Canalirogas* van Achterberg & Chen (although not in the type species) (van Achterberg & Chen, 1996). *Batotheca* and *Spinariella* exhibit an 'intermediate' condition, which suggests the character has been interpreted too simply in the past. In these taxa, the dorsal carinae seem to split near the base with the inner branches fusing and giving rise to a mid-longitudinal carina, whereas the outer branches run parallel for at least some distance towards the posterior of the tergite (see figs 23, 28, 47 and 67 in van Achterberg, 2007). In *Conspinaria*, there is a strong mid-longitudinal carina as well as strong, separated dorsal carinae running separately to the posterior margin of the tergite (see figs 311 in Chen & He, 1997 and 83 in van Achterberg, 2007). We interpret this as indicating that in the Spinariina+*Rogas* clade, the dorsal carinae split close to the base and in most species the anterior part of the inner branches, before they unite to form a mid-longitudinal carina, are reduced or completely lost. We therefore suggest that the clade Spinariini+*Rogas* be referred to as the '*Rogas*/*Spinaria*' genus group and that formal subtribes within Rogadini be abandoned.

Troporhogas was originally described from four species from Sri Lanka (Cameron, 1905). One of the species originally included was transferred to *Canalirogas* by Long & van Achterberg (2015), but the others all appear to be congeneric. Here, we included one of the Sri Lankan species, which shares relevant characters with the type species. This species was recovered as derived within the more widespread S.E. Asian *Iporhogas* with 98/98 support (Fig. 7) and that is not surprising as they are morphologically very similar. Indeed, both genera key to *Iporhogas* in Chen & He (1997). Described species of *Iporhogas* and *Troporhogas* are typically rather boldly patterned, often with a bicoloured, black and white metasoma (Long, 2014), and both have curved and either entirely (*Troporhogas*) or partly (*Iporhogas*) glabrous hind tibial spurs, and usually conspicuously transversely striate face, frons and occiput. *Troporhogas tricolor* Cameron, the type species, has a distinct mid-longitudinal carina on the median area of the metanotum, but this character can be variable among species in the genus. We therefore formally synonymize *Iporhogas* Granger with *Troporhogas* Cameron, **syn.n**.

Monophyly of Yeliconini

Our results (Fig. 10) disagree with those of Jasso-Martínez *et al.* (2021) in that Yeliconini were recovered as a monophyletic group (with support of 95 for the IQ TREE and TFE 96.95 for the RAXML-NG tree) rather than as a grade taxon. Morphologically, it is difficult to argue either way because the modifications of legs and head in both the Betylobraconi and Yeliconini make the assessment of affinities very difficult (see Quicke & Butcher, 2015; Butcher & Quicke, 2015a).

Host associations

Table S4 presents what is known about the host relationships of rogadines based on reliable data. It should be noted that many published host records for parasitic Hymenoptera are unreliable due the variety of reasons discussed by Noyes (1994) and Shaw (1994, 1997a). Therefore, we only deal with verified records here.

Members of the Aleiodini (in effect, *Aleiodes*) are predominantly solitary parasitoids of Noctuidae, Notodontidae, Erebidae (including Hypeninae, Lymantriinae, Arctiinae, Hypenodinae), Lasiocampidae and Geometridae, with a few confirmed records from a variety of other Lepidopteran families: Drepanidae (including Thyratirinae), Hesperiidae, Lycaenidae, Nymphalidae (Satyrinae), Pterophoridae, Sphingidae, Ypsolophidae and Zygaenidae (Shaw, 2006; Fortier, 2009; Shimbori & Shaw, 2014; van Achterberg & Shaw, 2016). A few species are known to be highly gregarious parasitoids of large noctuid caterpillars (Shaw, 2006). As noted by Zaldívar-Riverón *et al.* (2008: 14), published host records for *Heterogamus* are 'almost certainly erroneous and have never been repeated' and one has been shown to be a misidentification of an *Aleiodes* species with a particularly short second submarginal fore wing cell. No host records for this genus have been obtained despite extensive caterpillar rearing programs at sites where the adult wasps are frequently collected at light, including in the UK, Area de Conservación Guanacaste (ACG), Costa Rica, Papua New Guinea and Thailand. It appears that hosts of *Heterogamus* are not readily collected or reared.

Based only on the knowledge of *Yelicones* and *Pseudoyelicones*, Yeliconini appear to be exclusively parasitoids of phycitine and epipaschiine Pyralidae (Quicke & Kruft, 1995; Quicke *et al.*, 2018; Sharkey *et al.*, 2021) whose larvae are web building and often group-living. Their attack of web-building hosts has been supposed as responsible for the evolution of their robust legs as an adaptation to forcing their way to the host in its snarl of silk and leaves (Quicke, 2015).

Rogadini are predominantly parasitoids of Limacodidae, Zygaenidae, Dalceridae, Megalopygidae, Drepanidae and some ecologically similar Lycaenidae and Riodinidae. However, members of the *Colastomion* group have been reared from Erebidae, Crambidae, Uraniidae, Geometridae, Sphingidae and Lymantriidae, a range similar to that of Aleiodini. Interestingly, Old World species classified as *Macrostomion*, based on several published records, have only been reared as gregarious parasitoids of Sphingidae (Shaw, 2002; Maeto & Arakaki, 2005), whereas the hosts of New World *Macrostomion* are unknown; the record from Uraniidae by Janzen & Hallwachs (2017) refers to a species now classified in *Bioalfa* (Table S4). The large NW clade of *Triraphis* was further divided into two clusters: One clade includes all but one of the species reared from butterfly caterpillars (Riodinidae and Lycaenidae), whereas the lower group includes only one butterfly parasitoid (*T. matssegnestami*) as the remaining 10 are from moths, mainly Limacodidae, Megalopygidae and Zygaenidae. The New World Stiropiini, a group of very small-bodied rogadines (body length less than 3 mm), are exclusively parasitoids of leaf-mining Lepidoptera

larvae (Whitfield, 1988; Shaw, 1997b). Among the genera of Clinocentrini, only *Clinocentrus* has any host records and these are predominantly semi-concealed microlepidopteran larvae, Records from Coleoptera (see Yu *et al.*, 2016) are highly anomalous and need to be confirmed. There are as yet no host records for any Betylobraconini.

Taxonomy

The family group name Aleiodini was made available by Muesebeck (1929) through his use of Aleiodinae (Wharton & van Achterberg, 2000). The name has been used in a number of works (e.g. Zaldívar-Riverón *et al.*, 2008; Butcher & Quicke, 2011; Butcher *et al.*, 2014; Shaw *et al.*, 2020; Jasso-Martínez *et al.*, 2021), but no formal diagnosis has been provided. We therefore provide a formal diagnosis here.

Tribe **Aleiodini** Muesebeck

Diagnosis. Claws always without angular basal lobe. Vein m-cu of fore wing straight or nearly straight and forming an abrupt angle with 1-Cub (=2-CU1). Hind tibial spurs more or less straight and evenly setose. Propodeum without areola, usually with a distinct mid-longitudinal carina anteriorly (rarely absent), never with the mid-anterior pair of submedial, posteriorly diverging carina; if otherwise (densely vertically setose, with glandular areas or with strong bisinuate transverse carina, then the fore wing vein r-rs arising from the base of pterostigma). Dorsal carinae of first tergite uniting to form a triangular or evenly curved or less commonly tridentate shape. Hypopygium nearly straight ventrally, never strongly curved.

Afrorogas Quicke **gen.n.**

Type species. *Afrorogas copelandi* Quicke **sp.n.**

ZooBank registration: urn:lsid:zoobank.org:pub:31A27A4C-4936-47F3-B48C-E4985FC4DAF6

Diagnosis. The new genus is morphologically similar to *Orthorhogas* but differs in having a complete prepectal carina. In addition, the basal lobes of the claws are distinctly though weakly angulate. Median area of metanotum with a median carina. Hind tibia with the comb of specialized setae apicomedially. Hind tibial spurs straight and setose. Dorsope deep. Mediobasal triangular area of metasomal tergite 2 wide but short. Second to fifth tergites with sharp lateral crease. Hypopygium strongly convex. Ovipositor strongly down-curved.

Description. Head. Median flagellomeres elongate parallelogram-shaped. Labial and maxillary palps with four and six segments, respectively, normal, not swollen. Eyes glabrous, distinctly emarginate. Width of head: width of face: height of eye = 2.5: 1.0: 1.4. Malar suture present. Mandibles twisted so only one tooth visible in anterior view. Palps moderately slender. Frons flat with broad, with weak mid-longitudinal sulcus, without carina parallel to eye. Occipital carina strong and lamelliform, absent ventrally where lamellar part remains well separated from hypostomal carina. Mesosoma. Largely coriaceous. Notauli narrow, deep, crenulated, meeting mid-posteriorly. Prepectal carina complete. Precoxal sulcus present, straight, with coarser sculpture than surrounding mesopleuron. Scutellar sulcus wide with single strong mid-longitudinal carina. Medial area of metanotum with distinct mid-longitudinal ridge/carina. Propodeum anteromedially with short, submedial pair of weakly diverging carina and distinct mid-longitudinal. Wings. Fore wing vein m-cu weakly curved, forming a distinct angle with 1CUb. Hind wing vein M + CU distinctly longer than 1-M. Vein m-cu absent. Vein 1r-m oblique, joining R well before the separation of R1 and 1RS. Vein 1RS strongly curved; r-rs indicated by a distinct fold in the wing membrane. Legs. Claws with small, pointed, yellowish basal lobe. Hind coxa without a lamellar ridge dorsally. Inner apex of hind tibia with the comb of modified setae. Hind tibial spurs nearly straight, evenly setose. Metasoma. first tergite wide, approximately parallel-sided except for large subbasal semicircular emarginations; dorsal carinae uniting to form triangular area; dorsope large and moderately deep. Second tergite with medium-sized, mid-basal ovoid area giving rise to mid-longitudinal carina that is only slightly more conspicuous than other longitudinal striation. Striation of third tergite curved and diverging posteriorly. Hypopygium large and strongly curved ventrally. Ovipositor strongly down-curved, tapering evenly from deep base to tip; exserted part approximately as long as hind basitarsus.

Etymology. Name based on Africa and the genus *Rogas*.

Comments. Despite apparently being closely related to *Orthorhogas* (known only from Madagascar), it does not key there at couplet 11 in van Achterberg's (1991) key to African Rogadinae genera because it has a complete and strong prepectal carina – the other characters in that couplet are all variable among taxa that key out later. It does not fit well with either option at couplet 15. The claws have a distinct, angular but not large basal lobe and fore wing vein m-cu is hardly curved and not gradually merging with 2-CU1. However, it does have a distinct malar suture and comb of specialized setae at the apex of the hind tibia. As none of the genera from couplet 20 onwards (most of Aleiodini) have any pointed basal lobe and all lack a malar suture, the new genus would run to couplet 15 but also without any clear final conclusion. Its strongly enlarged and ventrally curved hypopygium and robust, strongly down-curved ovipositor are characteristic of the *Colastomion* group of genera and also of *Orthorhogas* Granger. In our analyses, it was recovered as the sister group to *Orthorhogas* but with very little support, and it differs from that in having a well-developed prepectal carina (absent in *Orthorhogas*) and metasomal tergites 3–5 striate (longitudinally and transversely) rather than smooth in *Orthorhogas*. However, it shares with *Orthorhogas* more or less straight and setose hind tibial spurs, relatively short and weakly but distinctly subbasally narrowed first metasomal tergite and the dorsolateral carinae of first tergite at the level of dorsopes, ventrally thin, forming large, crescent-shaped, transparent window. The latter character is shared by most members of the *Colastomion* group of genera, but the window is smaller due to their subbasally far narrower first tergite.

We have seen two undescribed *Orthorhogas* species from Madagascar; both possess weak but distinct traces of a prepectal carina laterally though not ventrally; therefore, the complete absence in the type species and the other undescribed one

sequenced here is presumably just a more derived state of character reduction.

Note that the sequence data were published as part of Hrcek et al.'s (2011) study. At that time, its identification was left simply as Rogadinae because of the taxon's uncertain generic placement, although it bore some similarity to *Canalirogas* in that it has traces of diverging, curved sculpture on metasomal tergites.

Afrorogas copelandi Quicke **gen.n.** and **sp.n.** (Figs 11, 12)

ZooBank registration: urn:lsid:zoobank.org:pub: BA6E777F-4FF0-4A99-937D-E741669E5385

Material examined. Holotype female, Kenya, Nyanza, Ruma National Park, Nyati Camp, 1240 m, 0° 39′ 28″ S 34° 19.422 E, 1-15.i.2006, Malaise trap, col. R. Copeland (DNA voucher BCLDQ00908; COI: BOLD:AAH8824; GenBank Accession No. JF271512) (NMK). Paratype ♀ Kenya, Nyanza, Ngoye, 0° 36 S 34° 05 E, 1147 m, 'in woodland next to grassland', col. R. Copeland. (DNA voucher BCLDQ00823; 28S: GenBank Accession No. JF415910; COI: GenBank Accession No. JF415906) (NMK).

Diagnosis. As for generic diagnosis. In addition, wings yellowish hyaline weakly infuscate on apical half. Body pale yellow. Mesosoma distinctly matt. Mediobasal area of tergite 2 wide but short.

Description. *Measurements of types*. Holotype: length of body 6.2 mm of fore wing 6.0 mm; paratype: length of body 7.7 mm of fore wing 6.0 mm. Head. Antennae broken, maximum of 32 flagellomeres remaining. Median flagellomeres 2.5 × longer laterally than wide. First flagellomere 1.2 and 1.4 × longer than second and third, respectively. Face shiny with weak transverse-coriaceous microsculpture. Intertentorial distance 2.6 × tentorio-ocular distance. Terminal segment of maxillary palp 0.85 × penultimate segment. Frons, vertex and occiput with traces of transverse microsculpture. The shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0: 2.0: 1.6. Length of eye in dorsal view 3.0 × length of head behind eye. Mesosoma. Mesosoma 1.4 × longer than high. Mesopleuron coriaceous, with fine, curved longitudinal striation dorsally and stronger longitudinal striae arising from prepecta carina. Propodeum anteromedially with mid-longitudinal carina, irregular, nearly complete, running anteriorly from mid-posterior part. Wings. Lengths of forewing veins r-rs: 3RSa: 3RSb = 1.0: 2.5: 4.3. Lengths of forewing veins 2RS: 3RSa: rs-m = 1.2: 1.8: 1.0. Vein 1CUb 13 × longer than 1CUa. Hind wing vein M + CU nearly 1.2 × length of 1-M. Legs. Length of fore femur: fore tibia: fore tarsus = 1.0: 1.05: 1.15. Length of hind femur: hind tibia: hind tarsus = 1.0: 1.1: 1.2. Hind basitarsus 12 × longer than wide. Metasoma. First tergite 1.5 × longer than posteriorly wide. First and second tergites with strong longitudinal striation separated by granulate microsculpture. Third tergite with curved, posteriorly diverging striation. Fourth–sixth tergites with increasingly fine irregular transverse striation. Lateral crease well developed on tergites 2 and 3 but very weak or indistinct on tergites 4–5. Colouration. Entirely ochreous yellow except flagellum and ovipositor sheaths black. Wing membrane hyaline with yellow tinge. Venation pale brown

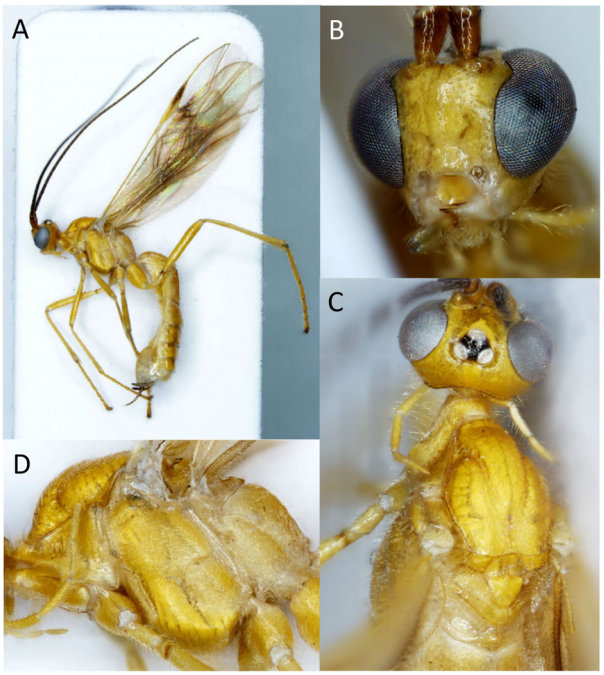

Fig. 11. *Afrorogas copelandi* **gen.n.** and **sp.n.**, holotype ♀. (A) Habitus, lateral view; (B) face, slightly oblique view; (C) head and thorax, near dorsal view; (D) mesosoma, lateral view.

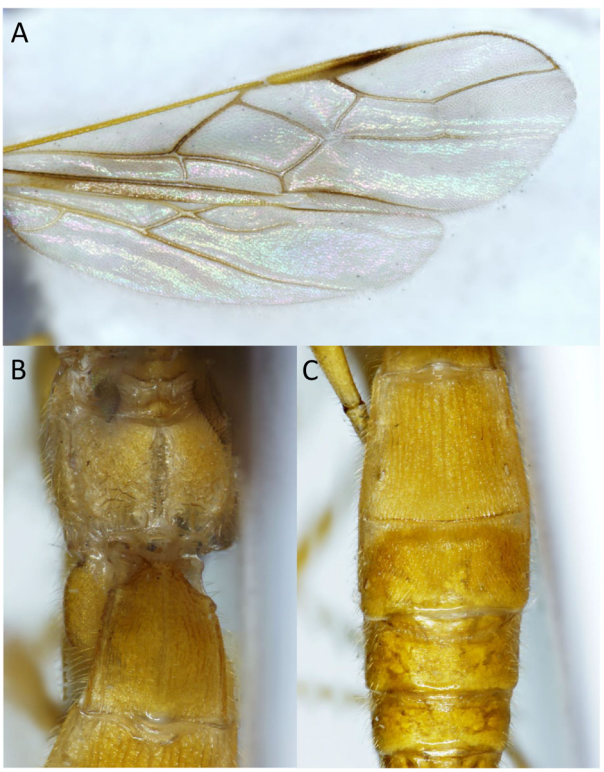

Fig. 12. *Afrorogas copelandi* **gen.n.** and **sp.n.**, holotype ♀. (A) Wings; (B) propodeum and first metasomal tergite, dorsal view; (C) metasomal tergites 2–5, dorsal view.

except fore wing vein C + SC + R and basal 0.5 of pterostigma pale yellow; apical 0.5 pterostigma black.

Etymology. Named after Robert S. Copeland (International Centre of Insect Physiology and Ecology, Nairobi) who has collected many interesting ad important specimens in Kenya.

Amanirogas Quicke **gen.n.**

Type species. *Amanirogas isolatus* Quicke **sp.n.**

ZooBank registration: urn:lsid:zoobank.org:pub: 07F2FC6F-5A6F-4701-9981-D5677FB30FEC

Diagnosis. The new genus is morphologically similar to *Korupia* in that the mandible has a narrow ventral flange, but differs in having a mid-longitudinal groove on the posterior third of metanotum, hind wing vein 1-rm strongly oblique and hind wing vein SR (=1RS) strongly curved basally. It is also similar to *Rogas* but differs in having the third segment of labial palp (of female) normal, robust, elongate but not strongly enlarged or flattened, and the dorsal carinae of the first metasomal tergite unite to define a triangular area. In addition, the basal lobes of the claws large and strongly angulate; median area of metanotum without complete median carina; hind tibia with the comb of specialized setae apicomedially; hind tibial spurs straight and setose; dorsope deep; second–fifth tergites with sharp lateral crease.

Description. Head. Median flagellomeres elongate. Eyes glabrous, distinctly emarginate. Malar suture present. Mandibles twisted so only one tooth visible in frontal view; with a narrow ventral flange. Maxillary and labial palps long and thin, not expanded, with six and four segments, respectively; terminal segment of labial palp short, 0.5 × length of preceding segment. Frons flat. Occipital carina complete, connected to hypostomal carina well removed from base of mandible. Mesosoma. Largely smooth and shiny with sparse setiferous punctures. Pronotum not strongly protruding in front of mesoscutum. Antescutal depression narrow, deep. Notauli deep anteriorly, complete, crenulate. Mesoscutal mid-pit present. Scutellar sulcus wide with single strong medial carina. Lateral carina of scutellum present on basal half. Prepectal carina complete. Precoxal sulcus short, discrete, crenulate. Propodeum largely areolate rugose with short mid-anterior longitudinal carina. Wings. Fore wing vein m-cu weakly-curved, forming a shallow angle with 1CUb. Hind wing vein M + CU approximately equal to 1-M. Vein 1r-m oblique, joining R well before separation of R1 and 1RS. Vein m-cu absent. Legs. Apex of hind tibia with the comb of specialized setae medially. Hind tibial spurs straight and setose. Claws with large, acute pointed basal lobe; brown with black margin. Metasoma. Dorsal carinae of first tergite united to form an anterior triangular area; dorsopes weak. Second tergite with distinct midbasal triangular area. Posterior margins of tergites 3–5 weakly convex. Tergites 2–5 (6 absent) with strong lateral crease.

Etymology. Named after the type locality and the genus name *Rogas*.

Comments. Note that the DNA of the type species was included in some previous papers under the generic name *Rogas* (DNA voucher nos. JM663 and AL0170; GenBank accession numbers – 28S: AJ784931, COI: AY935364) (Quicke *et al.* 2014). However, in none of those publications was it recovered as a clade with *Rogas luteus*, the type species of *Rogas*. The voucher specimen has just been relocated, and examination shows that indeed, it does not belong to *Rogas*, and in van Achterberg's (1991) key to Afrotropical Rogadinae genera, it keys reasonably straightforwardly to couplet 17 but clearly does not belong to either *Korupia* van Achterberg or *Rectivena* van Achterberg (see Diagnosis). In Chen & He's (1997) key to the Chinese genera of Rogadinae, it keys easily to *Rogasodes* Chen & He, and it is most similar to the closely related genus *Rhogasella* Baker, which is known only from the Philippines and Indonesia (Baker, 1917; Quicke & Shaw, 2005b). It differs from both of these in having the face not so strongly produced in front of the eyes and without stransverse sculpture, the ventrally strongly protruding clypeus and the short terminal article of maxillary palp, half length of preceding segment compared to equal to or longer than in *Rhogasella* and *Rogasodes*, respectively.

Molecular data from both sequenced gene fragments also provide unique apomorphies to justify the separation of *Amanirogas* **gen.n.** from *Rhogasella* and *Rogasodes*. The sequenced individuals of the latter two genera differ from *Amanirogas* and all other rogadines in the relatively conserved 2d′ and 3j′ stem regions of the 28S gene (Gillespie *et al.*, 2005): the 3′ base of 2d′ being an A in *Rhogasella* and *Rogasodes*, but it is a T in all others, and the second base of the 3j′ region is an A in *Rhogasella* and *Rogasodes* but a G in *Amanirogas* **gen.n**. and all other rogadines. In the COI gene, the 44th amino acid in the *Apis mellifera* reference sequence (NCBI: NC_001566) is a serine in *Rhogasella* and *Rogasodes*, but in *Amanirogas* **gen.n**. and all other rogadines, it is either aspartate, glycine or arginine.

Amanirogas isolatus Quicke **sp.n**. (Figs 13–15)

ZooBank Registration: urn:lsid:zoobank.org:act:0D4FACE5-B9C7-400E-B421-E767D5B6BC23

Material examined. Holotype, female (posterior of metasoma missing, see notes), Tanzania, Amani Hills, Amani Gate, 2001, col. D. Quicke. (CUMZ).

Diagnosis. As for generic diagnosis. In addition, wings yellowish hyaline weakly infuscate on apical half; body pale yellow; mesosoma distincly matt; notauli complete and crenulate; mediobasal area of tergite 2 wide but short.

Description. *Measurements of type*. Length of body (nearly complete) 4.4 mm, of fore wing 5.4 mm. Head. Antenna incomplete, with 28 remaining flagellomeres. Median flagellomeres 3 × longer than wide. First flagellomere 1.1 and 1.2 × longer than second and third, respectively, the last 2.5 × longer than wide. Face smooth and shiny with sparse setiferous punctures. Clypeus strongly protruding. Width of head: width of face: height of eye = 2.1: 1.0: 1.25. Intertentorial distance 5.0 × tentorio-ocular distance. Head short, 1.4 times wider than maximally long in dorsal view (length measured from occipital carina to front of face). Frons smooth, flat, with mid-longitudinal sulcus extremely weak. The shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0: 1.7: 2.0. Length of eye in dorsal view 3.3 × length of head

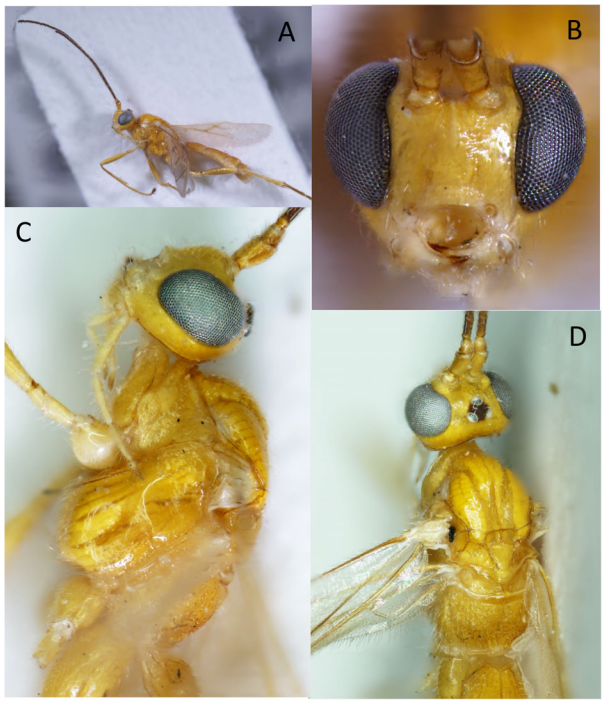

Fig. 13. *Amanirogas isolatus* **gen.n.** and **sp.n.**, holotype ♀. (A) Habitus, lateral view; (B) face, front view; (C) head and mesosoma, lateral view; (D) head and mesosoma, slightly oblique dorsal view.

behind eye. Occiput smooth and shiny without striations. Occipital carina strong, forming a laterally protruding flange. Mesosoma. Mesosoma 1.4 × longer than high. Mesopleuron and mesosternum smooth and shiny, with sparse setiferous punctures. Precoxal sulcus short, narrow, crenulated. Posterior margin of propodeum with numerous strong, long crenulations. Wings. Fore wing vein cu-a virtually interstitial with vein 1-M. Lengths of fore wing veins r-rs: 3RSa: 3RSb = 1.0: 2.0: 5.5. Lengths of forewing veins 2RS: 3RSa: rs-m = 1.5: 2.0: 1.0. Hind wing vein M + CU approximately same length as 1-M. Legs. Lengths of fore femur: tibia: tarsus = 1.0: 1.2: 1.25. Hind basitarsus 7.5 × longer than wide. Metasoma. first tergite 1.15 × longer than posteriorly wide. second tergite 2.0 × longer than third, 1.4 × longer than apically wide. All tergites with parallel longitudinal striation, though that on the medial parts of tergites 4 and 5 relatively weaker than laterally. Colouration. Ochreous yellow except flagellum and stemmaticum black, palps cream-coloured, distal segment largely infuscate, hind tarsus infuscate. Wings hyaline, with pale brown venation and pterostigma.

Etymology. Name refers to isolated position of this species.

Comments. The sixth tergite, hypopygium, ovipositor and venom apparatus are absent from the mounted holotype specimen, and the venom apparatus was prepared as a microscope slide as part of the comparative study of Zaldívar-Riverón *et al.* (2004). Sequence data for this specimen were included in earlier phylogenetic studies (Quicke *et al.*, 2014).

Papuarogas Quicke **gen.n.**

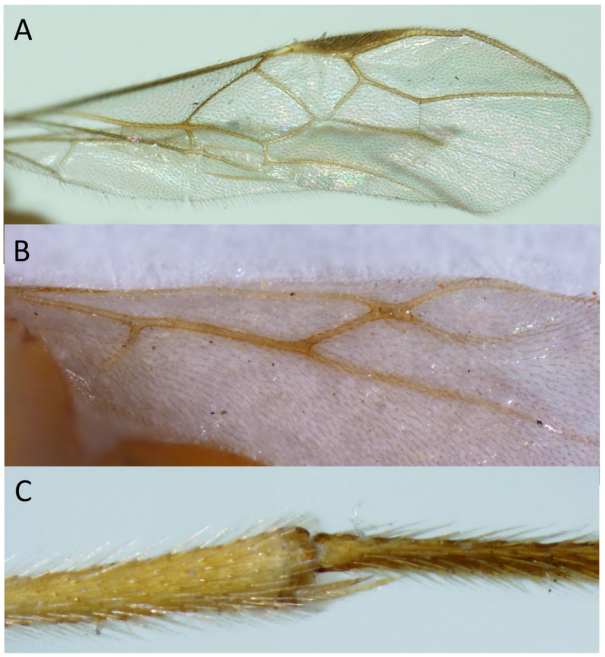

Fig. 14. *Amanirogas isolatus* **gen.n.** and **sp.n.**, holotype ♀. (A) Fore wing; (B) most of hind wing; (C) apex of hind tibia showing setose, nearly straight, spurs.

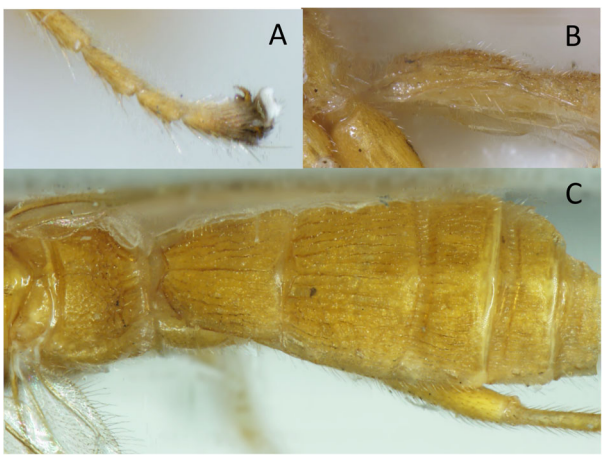

Fig. 15. *Amanirogas isolatus* **gen.n.** and **sp.n.**, holotype ♀. (A) Terminal tarsal articles and claw of fore leg; (B) first metasomal segment lateral view; (C) propodeum and metasoma, dorsal view.

Type species: *Papuarogas dameni* **sp.n.**

ZooBank registration: urn:lsid:zoobank.org:pub:04B554C9-E9A6-4F53-9693-93B066176A18

Diagnosis. The new genus is morphologically similar to *Troporhogas* Cameron, but differs in having the top of the head shiny and face without striation and in having the area formed by unison of the dorsal carinae with four posterior segments, and the midbasal area on second tergite being wide with four-sided posterior margin.

Description. Head. Terminal flagellomere pointed, not acuminate (compressed in holotype, but this may be a postmortem distortion). Median flagellomeres elongate, somewhat rhomboidal. Eyes glabrous, distinctly emarginate. Face smooth and shiny. Malar suture present. Mandibles bidentate but twisted so only one tooth visible in frontal view. Occipital carina strong and complete, joining hypostomal carina before the base of mandible. Labial and maxillary palps with four and six segments, respectively, normal, not swollen. Eyes glabrous, distinctly emarginate. Frons flat, with distinct carina running subparallel to and slightly removed from eye. Mesosoma. Largely smooth and shiny. Notauli weakly impressed anteriorly, smooth; mid-posterior part of mesonotum longitudinally striate. Scutellar sulcus wide and deep with a strong mid-longitudinal carina. Prepectal carina complete. Precoxal sulcus weakly impressed, curved weakly crenulate. Median area of metanotum with distinct mid-longitudinal carina. Propodeum coarsely sculptured, with the pair of posteriorly diverging, weak carinae arising from mid-anterior margin. Wings. Hind wing vein 1RS + 2RS nearly straight, vein r-rs present as a distinct sharp fold in wing membrane. Vein m-cu absent. Vein 1r-m oblique, joining R well before separation of R1 and 1RS. Legs. Claws with large rounded basal lobe. Apex of hind tibia with the dense comb of specialized setae on inner margin. Hind tibial spurs strongly curved and glabrous. Metasoma. Dorsal carinae formed into four sections, their median confluence giving rise to mid-longitudinal carina. Dorsopes deep but well separated medially. Second tergite with a large mid-basal area. Posterior margins of tergites 3–5 weakly convex. Ovipositor short, slender and straight.

Etymology. Named after country of origin, Papua New Guinea, and the genus name *Rogas*.

Comments. The examined specimens of *Papuarogas* **gen.n.** came from a caterpillar rearing campaign in Papua New Guinea (Novotny *et al.*, 2010; Hrcek *et al.*, 2011; Whitfeld *et al.*, 2012). A female specimen representing a separate species from the type species was included in the analyses (Papua New Guinea, Madang, 5.23087978°S, 145.1820068°E, 100 m, specimen voucher USNM-ENT-00680050 (BOLD voucher ASQSP085-08; COI GenBank Accession No. JF962612) (USNM), but is not being formally described here because the remaining specimen is highly fragmented, with wings and most of mesosoma missing. It was also reared from Geometridae, in this case most likely *Jodis albifusa* (Warren) collected on *Pometia pinnata* J.R.Forst. & G.Forst (Sapindaceae). The sequence data for this specimen were published on GenBank under the name '*Aleiodes* sp. MAS-2011' a broad study of the utility of COI for phylogenetics by Quicke *et al.* (2012d). Both known species were reared from mummified Geometridae caterpillars.

Papuarogas dameni Quicke **sp.n.** (Figs 16, 17)

ZooBank Registration: urn:lsid:zoobank.org:act:639E57D4-7DFA-46DC-8315-E9900C7B4134

Material examined. Holotype, ♀ Papua New Guinea, Madang, 5.23087978°S, 145.1820068°E, 100 m specimen voucher USNM-ENT-00680137 (BOLD voucher ASQSP022-08; COI GenBank Accession No. JF963815) (USNM).

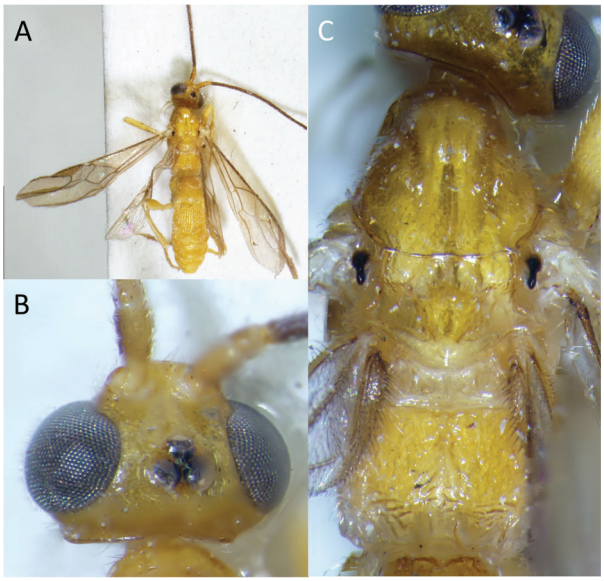

Fig. 16. *Papuarogas dameni* **gen.n.** and **sp.n.**, holotype ♀. (A) Habitus, dorsal view; (B) head, nearly dorsal view; (C) mesosoma, dorsal view.

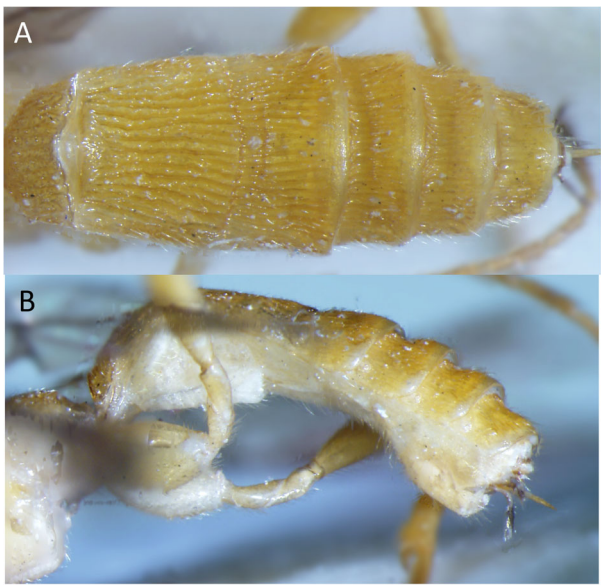

Fig. 17. *Papuarogas dameni* **gen.n.** and **sp.n.**, holotype ♀. (A) Metasoma, dorsal view; (B) metasoma, lateral view.

Diagnosis. As for generic diagnosis. In addition, flagellum dark brown-black (pale yellowish brown in undescribed species '*Papuarogas* sp. 1'); setiferous punctures on upper part of face not confluent (confluent and forming distinct subhorizontal lines in '*Papuarogas* sp. 1').

Description. *Measurements of type*. Length of body 4.8 mm, of fore wing 4.5 mm, of antenna 6.9 mm. Head. Median flagellomeres 2.8 × longer than wide. Width of head: width of face: height of eye = 2.3: 1.0: 1.3. Face shiny with some deep setiferous punctures, especially medio-dorsally. Intertentorial

distance 2.5 × tentorio-ocular distance. The shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0: 2.0: 1.5. Frons flat with very weak mid-longitudinal sulcus. Length of eye in dorsal view 4.3 × length of head behind eye. Mesosoma. Mesosoma 1.5 × longer than high, shiny. Notauli impressed and crenulated, reaching posterior 0.4 of mesoscutum; posteromedially mesoscutum with several longitudinal depressions and long narrow mid-pit. Propodeum with weak pair of anteromedial carinae diverging posteriorly and demarking a narrow 'V'-shaped zone; anterolaterally with large confluent punctures, mediolaterally becoming irregular transverse rugae; posteriorly with numerous, strong crenulae. Wings. Fore wing vein cu-a weakly postfurcal, vein 1Cub 7.5 × 1CUa. Lengths of forewing veins r-rs: 3RSa: 3RSb = 1.0: 5.0: 7.0. Lengths of forewing veins 2RS: 3RSa: rs-m = 1.0: 1.3: 2.7. Hind wing vein M + CU 1.3 × 1-M. Legs. Lengths of fore femur: tibia: tarsus = 1.0: 1.15: 1.2. Lengths of hind femur: tibia: tarsus = 1.0: 1.1: 1.25. Hind femur somewhat swollen, 10 × longer than wide. Hind basitarsus 8.0 × longer than wide. Metasoma. Tergites 1–3 coarsely longitudinally striate; mid-longitudinal carinae of tergites 1 and 2 hardly more prominent than other striae. First tergite 1.14 × longer than posteriorly wide. Second tergite 1.6 × longer than third, with median part of midbasal area somewhat sculptured. Tergites 4 and 5 with strongly striate transverse subbasal groove, the remainder striate laterally, smooth medially. Exserted part of ovipositor less than 0.5 length of hind basitarsus. Colouration. Ochreous yellow, flagellum black, hind tarsi infuscate. Wing membrane pale brown, wing venation, including pterostigma, darker brown.

Etymology. Named after Philip Damen, leader of Wanang village.

Comments. Both COI and 28S-D2 DNA sequences were submitted to GenBank under the name 'Rogadinae sp.' as part of a broad study of the utility of COI for phylogenetics by Quicke *et al.* (2012d). Excluded from the type series is a very fragmented specimen, voucher USNM-ENT-00681531 (BOLD: ASPNI820-09), which is probably the same species as indicated by its sequence data, and was reared from the same caterpillar morphospecies and off the same tree species. Reared from Geometridae caterpillars, most likely belonging to the *Albinospila syntyche* Prout complex, collected on *Mallotus peltatus* (Geiseler) Müll.Arg. (Euphorbiaceae).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Annotated 28S rDNAgene sequences showing secondary structure interpretations are shown, and aligned positions are coded 'p', 'u' and 'x' for pairing, unpairing and ambiguously alignable (excluded) bases, respectively.

Appendix S2. Annotated 16S rDNAgene sequences showing secondary structure interpretations are shown and aligned positions are coded 'p', 'u' and 'x' for pairing, unpairing and ambiguously alignable (excluded) bases, respectively.

Figure S1. 16S_IQTree2_UFbootstraps.pdf

Figure S2. 16S_Raxml-NG_FBPsupports.pdf

Figure S3. 16S_Raxml-NG_TBEsupports.pdf

Figure S4. 28S_IQTree2_UFbootstraps.pdf

Figure S5. 28S_Raxml-NG_FBPsupports.pdf

Figure S6. 28S_Raxml-NG_TBEsupports.pdf

Figure S7. COI_IQTree2_UFbootstraps.pdf

Figure S8. COI_Raxml-NG_FBPsupports.pdf

Figure S9. COI_Raxml-NG_TBEsupports.pdf

Figure S10. EF1a_IQTree2_UFbootstraps.pdf

Figure S11. EF1a_Raxml-NG_FBPsupports.pdf

Figure S12. EF1a_Raxml-NG_TBEsupports.pdf

Figure S13. FourGenes_IQtree2_UFbootstraps.pdf

Figure S14. FourGenes_Raxml-NG_FBPsupports.pdf

Figure S15. FourGenes_Raxml-NG_TBEsupports.pdf

Figure S16. Photomicrograph of male metasomal tergal gland pores of *Aleiodes pammitchellae* voucher DHJ-PAR0062179.

Figure S17. Photomicrograph of male of *Aleiodes masneri* (van Achterberg, 1991) comb n. (=*Rhinoprotoma masneri* van Achterberg), DNA voucher NZAC04034848 [reproduced under Creative Commons Licence Non-Commercial Share Alike, via BOLD.]

Table S1. GenBank accession numbers for gene fragments included in molecular phylogenetic analyses. Where two accession numbers are given, sequences from two partially overlapping reads were combined to give a longer read.

Table S2. Details of species groups and sequence selection for the representatives of *Aleiodes*.

Table S3. Details of taxa for which specified gene sequences were extracted and assembled from genomic libraries.

Table S4. Host groups recorded for species or genera of Rogadinae included in this study.

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Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article

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