

Origin and diversification of hoverflies: a revision of the genera *Asarkina* and *Allobaccha* - A BIG4 Consortium PhD project

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Abstract

This BIG4 PhD project involves the overall taxonomic revision of the genera *Allobaccha* Curran and *Asarkina* Macquart (Diptera: Syrphidae). The revisions will be divided by biogeographic region (Afrotropical and Indomalayan) and published accordingly. The publications will be collated as a thesis for submission to the University of Bonn (Rheinische Friedrich-Wilhelms-Universität Bonn, Germany) doctoral program of biology. The goal of this project is to resolve alpha taxonomy and to infer the phylogenetic placement of these genera within the Syrphidae using Next-Generation Sequencing and Anchored Hybrid Enrichment techniques. The techniques undertaken in this project will be applied to future systematic problems in Diptera and testing future phylogenetic hypotheses.

Keywords

Diptera, Syrphidae, *Allobaccha*, *Asarkina*, entomology, systematics, phylogenomics, taxonomy, bioinformatics, next-generation sequencing, anchored hybrid enrichment, BIG4 consortium.

Objectives, Concept and Approach

The central objective of the [BIG4 Systematics consortium](#) is to imbue 15 doctoral students with the latest techniques required to carry systematic entomology into the future. Focused on the big four orders of insects (Diptera, Hymenoptera, Lepidoptera, and Coleoptera) students will combine the latest techniques in genomics, phylogenetics, bioinformatics, computer-enhanced drawing, and taxonomy with semantic biodiversity publishing and citizen science, into highly competitive cross-disciplinary training program with a stronghold in biosystematics and with a wide scope of complementary skills transferrable to other science disciplines, business, or industry. Successful students are expected to develop skills that will allow them to lead and coordinate large scale, global systematic projects involving many colleagues from a multitude of disciplines. Over the course of completing their own projects students will learn the practical value of inter-disciplinary methodology and collaboration with project cohorts and senior colleagues, to develop global relationships with entomological researchers, academics, private enterprises, bioinformaticists, and science publishers over the course of their project, thereby enhancing their postdoctoral impact in the field for years to come.

Project description

The pivotal goal of this PhD is to address long-standing problems with the alpha taxonomy of two genera of flower flies (Diptera: Syrphidae), *Allobaccha* Curran, 1928 and *Asarkina* Macquart, 1834. Syrphidae is one of the most diverse families of Diptera and very attractive for citizen-scientists. Adults are important pollinators in natural and agricultural environments and larvae are used in the biological control of some crop pests and are important organic matter recyclers. Although they have been studied for a long time, phylogenetic relationships of its main subfamilies and genera are not totally understood; this is especially the case of large genera of flower flies, such as *Allobaccha* and *Asarkina*. The goals of this PhD is to taxonomically revise both genera using new publishing tools, as well as to study their phylogenetic placement among other Syrphidae using molecular data. This will provide a better understanding of the evolution of the feeding modes of the immature stages, which might be applied in biological control and assisted-pollination in greenhouses.

Background

The Syrphidae (Insecta: Diptera) are a large (6000+ recognized species; 200+ genera) and variable fly family commonly called hoverflies in Britain and the rest of Europe and flower flies in North America. These “true flies” are well known pollinators of crops and natural plants (Ssymank and Kearns 2009, Inouye et al. 2015) and their economic importance cannot be overstressed. Adults feed mostly on pollen and nectar and have been used as bioindicators as well to assess biodiversity loss and the efficiency of restoration and conservation policies (Sommaggio 1999, Tschardt et al. 2005, Ricarte et al. 2011,

Sommaggio and Burgio 2014). Exhibiting Batesian mimicry they tend to be brightly colored, yellow, orange, pale brown, or blue, against a variety of dark maculation patterns, modeled after Hymenoptera. The spurious vein is the most obvious and frequently used feature to diagnose this family, although some species lack it. In larval state, they exhibit a large array of lifestyles, playing an important role as biological control agents of pests (Schmidt et al. 2004, Bergh and Short 2007, Nelson et al. 2012, Eckberg et al. 2015) and recycling leaf litter and other organic matter (Lardé 1989, Rotheray et al. 2009, Morales and Wolff 2010, Martínez-Falcón et al. 2012). At present there are four recognized subfamilies: Eristalinae, Microdontinae, Pipizinae, and Syrphinae (Mengual et al. 2015). This PhD gives particular focus to the Syrphinae. Syrphinae are a widespread subfamily, found in all the Biogeographic Regions. They can be distinguished from other syrphid subfamilies by: the absence of pile on the postpronotum, head posteriorly strongly convex and closely appressed to thorax so that postpronota are partly or entirely hidden, and male abdomen with tergum 5 visible in dorsal view. Immature stages of Syrphinae are mostly predators on several kinds of prey (Rojo et al. 2003), although some species of the genera *Toxomerus* Macquart, 1855 and *Allograpta* Osten Sacken, 1875 are secondarily phytophagous, either pollen-feeders or leaf-miners and stem-borers (Nishida et al. 2002, Weng and Rotheray 2009, Reemer and Rotheray 2009, Zuijlen and Nishida 2011, Jordaens et al. 2015a, Dumbardon-Martial 2016). Two genera from this subfamily are the focus of this PhD, namely *Allobaccha* Curran, 1928 and *Asarkina* Macquart, 1834. Both genera have in common that they occur in the Afrotropical, Indomalayan, Australasian and Eastern Palaearctic Regions, but they differ very broadly morphologically. *Asarkina* species are medium-sized to large with a produced lower face and a broad, very flat abdomen, which is almost entirely yellow or orange and has a strong margin (Macquart 1834 Vockeroth 1969). On the other hand, *Allobaccha* species are small- to medium-sized with a convex facial profile (facial tubercle not very marked), usually dark thorax and abdomen with pale markings, and abdomen without margin, weakly to strongly petiolate. Some Afrotropical species of *Allobaccha* have an infuscate pattern on their broadened wings.

The Afrotropical and Indomalayan Regions have been somewhat neglected or understudied during the last decades but it has seen a resurgence with a broader interest in syrphid workers since the 2010's (Doczkal et al. 2016, Jordaens et al. 2015a, Jordaens et al. 2015b, Mengual and Ghorpadé 2010, Mengual 2015, Mengual et al. 2013, Reemer and Hippa 2008, Thompson and Skevington 2014, Thompson 2013a, Thompson 2013b, Thompson 2013c, Thompson 2014, Thompson 2015, Steenis 2010, Steenis 2015, Mengual et al. 2008a, Mengual et al. 2008b, Mengual et al. 2012, Hippa et al. 2015, Whittington 2003, among others). *Allobaccha* and *Asarkina* are two such groups that need a thorough taxonomic review because the last taxonomic works are more than fifty years old (Curran 1927, Curran 1928, Curran 1938, Sack 1926, Keiser 1952, Keiser 1971). These genera have a convoluted taxonomic history mainly due to the lack of an overall and comprehensive treatment involving multiple approaches such as the use of genital characters and molecular data. *Allobaccha* and *Asarkina* belong to the tribe Syrphini, even though this tribe has been recovered non monophyletic in the last molecular analyses (Mengual et al. 2008a, Mengual 2015, Young et al. 2016). As such, the phylogenetic placement of these species-rich taxa is not yet resolved.

To date exterior adult morphology has been the primarily focus in developing species concepts in these genera (Brunetti 1929, Curran 1928, Dirickx 2010, Enderlein 1938, Keiser 1952, Vockeroth 1969, Ghorpade 1994). Yet, the species of both genera (*Allobaccha* and *Asarkina*) suffer from a poverty of consistent or diagnostic morphological characters. This has led to many synonyms and few incomplete and consistent identification keys (Curran 1927, Curran 1928, Curran 1938), although Dirickx (2010) did provide an excellent identification key to *Allobaccha* species of Madagascar. Vockeroth (1969) reviewed the tribe Syrphini very thoroughly and worldwide, including invaluable genus-level examination of the male genitalia and phylogenetic affinities based on adult morphology. Unfortunately a thorough examination of genitalia has never been undertaken to support species concepts in any of these two genera. Shatalkin (Shatalkin 1975a, Shatalkin 1975b) showed the usefulness of male genital morphology of many syrphid genera including both genera under review, though it is widely known that Syrphinae provide more subtle and discrete characters to select than other subfamilies.

The aim of this PhD project is to combine several sources of taxonomic information 1) to infer the phylogenetic placement and relationships of *Allobaccha* and *Asarkina* within Syrphinae, and 2) to review the species of both genera from the Afrotropical and Indomalayan Regions based on morphological characters, including male genitalia, with the help of DNA barcodes whenever possible. DNA barcodes are a small fragment of the cytochrome c oxidase subunit 1 gene that was postulated as species specific (Hebert et al. 2003). Barcode sequence data have been accumulated over the last 15-20 years for Syrphidae but the DNA barcode method has never been used to test species hypothesis for these genera. A first attempt to create a DNA barcode reference library for Afrotropical flower flies was carried out by Jordaens et al. (2015b). Nevertheless, some molecular data have been used to infer the phylogenetic placement of both genera (Mengual et al. 2008a, Mengual et al. 2008b, Mengual et al. 2012, Mengual 2015).

To infer the phylogenetic placement of these genera we will use massive parallel high-throughput sequencing, the so-called Anchored Hybrid Enrichment technique (Lemmon et al. 2012, Young et al. 2016). Anchored hybrid enrichment techniques are being used to generate a large, cost-efficient molecular dataset from hundreds of loci that can be used in phylogenetic systematics.

Overall, the present project integrates with the larger BIG4 consortium by jointly participating with the other 15 student candidates in an open access research space where peers can examine projects, with possibly new research directions suggested. Additionally, any new techniques in systematics can be outlined in an open information space with a dynamic methodology. This presents a unique opportunity for student researchers to present their progress with ongoing peer-review and scrutiny via the Pensoft Publishing portal (Senderov and Penev 2016). Projects overlapping allows participants and partners to develop more educational programs, workshops and courses for a variety of disciplines, in a very attentive and supportive learning environment, which would not necessarily be available to a single student candidate due to cost and time restriction.

Implementation

The success of this project requires the implementation of several work tasks that are broken down into smaller sub-tasks in order to better coordinate and manage the overall project. These tasks are thoroughly outlined in the following Methodology section.

Methodology

Material

Allobaccha and *Asarkina* comprise many species spanning several biogeographic regions. Initial efforts involve visiting museums to obtain loan material and cover all known and currently recognized species. Types are widespread in a variety of museums and collections throughout the world. Contacting collection managers and negotiating loans for this material or visiting these collections to examine specimens may be necessary if types are too fragile to travel or too numerous. In addition, some field trips are planned to collect fresh material for phylogenetics purpose, either DNA barcodes and/or New-Generation Sequencing (NGS).

Molecular Data

Most of the species of *Allobaccha* and *Asarkina* lack any molecular data, therefore gathering sequences and vouchers is an important first step. We have gained some material from field work or supplied mainly by colleagues within the cooperative framework of the collaborative project 'World Syrphidae Phylogeny' (http://www.canacoll.org/Diptera/Staff/Skevington/Syrphidae/Syrphidae_World_Phylogeny.htm), mainly Kurt Jordaens, Jeff Skevington, Martin Hauser, Ante Vujić, Menno Reemer, Axel Ssymank, Sander Bot, and Gunilla Ståhls among others. DNA barcodes generated during this project will be combined with previous work to explore the phylogenetic species concept in these genera. Furthermore, all specimens used in any molecular study in this project will be vouchered, properly curated, and databased with unique identifiers.

Using transcriptomic data supplied by the 1Kite project (Misof et al. 2014) for several flower fly species, multispecies baits will be designed to target and enrich several hundreds of orthologous genes using BaitFisher (Mayer et al. 2016). The obtained dataset, then, will be analyzed to infer phylogenetic relationships of the genera within the subfamily Syrphinae.

Morphology

Literature on taxonomy of Syrphidae will be studied and harvested for previously used morphological characters to distinguish species of both genera. Other morphological characters will be explored to support species hypotheses, e.g. high-resolution photography, micro-CT imaging if necessary for microstructures, new drawing techniques and the study of male genitalia. Compiled morphological information will be used to link sexes, male and female, of the same species and to define potential new and known species.

Work plan

Work task 1 : Information gathering: collect and review all relevant literature in order to compile information about *Asarkina* and *Allobaccha* and closely related groups, with focus on systematics, biology and ecology.

Sub-tasks: Generate a list of all species and synonyms and gather all related descriptions and translate as needed; note any keys provided or characters employed to diagnose species; create tentative checklist of recognized species.

Work task 2: Obtain as much specimen material as possible from a variety of museums and collections in order to cover the vast majority of their geographic distribution.

Sub-tasks: Label, sort, and examine the material and note any sequence vouchers; note geography, and tentative identifications; compare identifications with checklist of valid species and determine if any species are unavailable.

Sub-task: Track down and attempt to obtain type specimen loans, or make arrangements to visit collections to examine all type material available.

Work task 3: Sort all material by Biogeographic Regions (Afrotropical, Indomalayan).

Work task 4: Tentative diagnostic characters are to be assessed for *Allobaccha* species from the Afrotropical Region and a key generated based on the exterior morphology, noting any important secondary characters that might arise in descriptions.

Sub-task: Compare type specimens with morphospecies and discern any discrepancies between types and type descriptions, or types and examined specimens; associate morphospecies with type material and designate holotypes to any new species.

Sub-task: Test new identification key by dissecting and comparing male genitalia of each putative species. Revise species hypotheses as needed if the genitalia prove informative at the species level.

Sub-task: Species hypotheses resulting from morphological data will be tested using DNA barcodes; in the case of incongruence potential reasons will be explored.

Sub-task: Once the key is refined, descriptions and redescriptions will be written for all putative species, and they will be organized for a revision publication (See **Primary Publications** below).

Work task 5: Repeat Work task 4 for *Allobaccha* species from the Indomalayan Region.

Work task 6: Repeat Work task 4 for *Asarkina* species from the Afrotropical Region.

Work task 7: Repeat Work task 4 for *Asarkina* species from the Indomalayan Region.

Work task 8: Generate a phylogenetic hypothesis concerning the placement of *Allobaccha* and *Asarkina* within the Syrphidae using an orthographic prediction and analysis pipeline initially developed for the 1Kite (1K Insect Transcriptome Evolution) project (www.1kite.org).

Sub-task: Align transcriptomic data from 1Kite, including several species of Syrphidae belonging to the four subfamilies. Then, perform orthologous gene prediction on the ZFMK Cluster.

Sub-task: Use BaitFilter (Mayer et al. 2016) to search for orthologous genes within the genome of *Drosophila melanogaster* Meigen, 1830, and determine if any gene paralogs are present; if so, these are to be removed.

Sub-task: Design baits/probes for anchored hybrid enrichment from selected orthologous genes.

Sub-task: Wet lab work. Extract DNA from specimens of *Asarkina* and *Allobaccha*, closely related Syrphinae and selected outgroup taxa from multiple biogeographic regions; prepare samples with the newly designed baits, and sequence.

Sub-task: With the molecular data newly generated, the phylogenetic placement of *Asarkina* and *Allobaccha* within the Syrphinae will be inferred using phylogenetic software.

Sub-task: A manuscript will be prepared that describes the placement and phylogenetic relationships of *Allobaccha* and *Asarkina*.

Primary Publications

Phylogenetic relationships of superfamily Syrphoidea based on transcriptomic data from 1Kite.

A taxonomic revision of the genus *Allobaccha* of the Afrotropical Region.

A taxonomic revision of the genus *Allobaccha* of the Indomalayan Region.

A taxonomic revision of the genus *Asarkina* of the Afrotropical Region.

A taxonomic revision of the genus *Asarkina* of the Indomalayan Region.

Systematics and phylogenetic placement of *Asarkina* and *Allobaccha* .

Additional Goals

Some additional goals include 1) learning a variety of practical technical skills related to science in general and systematics in particular, such as SEM imaging, micro-CT scanning, computer-based scientific illustration, morphometrics, general coding for systematics and related problems, trait mapping, and a wide variety of approaches to phylogeny construction and analysis; 2) to acquire new knowledge on NGS and anchored enrichment techniques and analysis, bait design methodologies; and finally, 3) to gain experience on the overall coordination of large-scale, complex projects involving multiple

colleagues from many disciplines to address global problems in insect systematics. The education program outlined below is intended in part to facilitate these goals.

Educational Program:

Planned Courses, Conferences, Secondments, Field Collecting and visiting Museums

2015

Naturalis Biodiversity Center (Leiden, Netherlands); September 3 - 4, 2015: gaining loan material

Zoological Museum, University of Copenhagen (Copenhagen, Denmark); September 13-19, 2015: BIG4 "kick-off" workshop

Royal Museum of Central Africa - RMCA (Tervuren, Belgium); December 11, 2015: gaining loan and DNA material

Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Canada); October 12 to November 27, 2015: multigene extraction, sequencing, and alignment training

2016

Zoologisches Forschungsmuseum Alexander Koenig - ZFMK (Bonn, Germany); January 11-12, 2016: BASH and Cluster training

Indobiosys (Indonesian Biodiversity Discovery and Information System) (Java, Indonesia); April 1-May 5, 2016: field collecting

BIG4 bi-annual workshop (Havraníky, Czech Republic); June 5-12, 2016: training on Coleoptera, Diptera, Hymenoptera and Lepidoptera

cmt GmbH /ecSeq Bioinformatics (Munich, Germany); June 29-July 01, 2016: NGS and Analysis Workshop

ZFMK Scientific Advisory Committee (Bonn, Germany); September 30, 2016: Project poster presentation and independent review

BIG4 bi-annual workshop (Stockholm, Sweden); October 9-19, 2016: Bayesian statistics training and European Union mid-term evaluation

ZFMK (Bonn, Germany); October 16-November 11, 2016: PEARL training course

2017

Secondment 1: Royal Museum of Central Africa (Tervuren, Belgium); November-December 2017: practical wetlab: Streamlined COI Barcoding with Kurt Jordaens

9th International Symposium on Syrphidae (Curitiba, Brazil); August 28 – September 1, 2017: oral and poster presentations

2018

Secondment 2: Finnish Museum of Natural History (Helsinki, Finland); February 2018: practical museum curation and systematic phylogenetics: Specimen identification, preservation, data collection, collection management, and phylogenetic systematics of Diptera with Gunilla Ståhls

9th International Congress of Dipterology (Windhoek, Namibia); November 25-30, 2018: oral and poster presentations

Timeline and Workflow

Work program for 2015

Work task 1 (Completed)

Gather specimen material and any available sequence data (Completed)

Attend necessary meetings and available training in molecular laboratory techniques (Completed)

Work program for 2016

Create a PhD project plan (Completed)

Crash course in BASH and cluster use at ZFMK (Completed)

Syrphid collection training and tropical field experience in Java, Indonesia (Completed)

Attend ecSeq NGS and Analysis course in Munich, Germany (Completed)

Illustrate or photograph species or morphology as needed for figures (in process)

Work tasks 2 and 3 (Completed)

Work task 4 for the Afrotropical species of *Allobaccha*, and publish (in process)

Use ZFMK Cluster and 1Kite pipeline to design syrphid baits (Completed)

BIG4 bi-annual workshop on Bayesian statistics and European Union mid-term evaluation (Completed)

PEARL Training Course (Completed)

Work program for 2017

Work task 8 (Wetlab Completed; sub-tasks in process)

Work task 5 for the Indomalayan species of *Allobaccha*, and publish (in process)

Work task 6 for the Afrotropical species of *Asarkina*, and publish

Work program for 2018

Work task 7 for the Indomalayan species of *Asarkina*, and publish

Collate all publications into main body of doctoral dissertation

-Submit dissertation to Rheinische Friedrich-Wilhelms-Universität Bonn

Address needed revisions based on supervisor feedback

-Defend Dissertation and submit final Doctoral Dissertation to the Rheinische Friedrich-Wilhelms-Universität Bonn

Obtain a Doctoral Degree in Biology

Expected results and impact

Expected results include the publication of four taxonomic revisions (*Allobaccha* and *Asarkina* of the Afrotropical and Indomalayan regions), with possible implications for the Australasian and Palaearctic Regions. An article will be published on the placement and phylogenetic relationships of *Allobaccha* and *Asarkina*, which will outline novel next-generation sequencing techniques and anchored-enrichment approaches, with newly designed syrphid baits which will become the standard protocol used to generate future large-scale molecular datasets.

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Christoph Mayer, Oliver Niehuis, Alexander Donath and Malte Petersen were invaluable in developing the orthography pipeline and continue to provide direction on the genome annotation and alignments and bait design techniques.

Thomas Dieter Pauli has been indispensable in assisting in the technical aspects of coding for bait design and incorporating multi-gene primers from concurrent projects. Jeff Skevington and Scott Kelso provided multi-gene sequences from the ongoing Phylogeny of World Syrphidae (http://www.canacoll.org/Diptera/Staff/Skevington/Syrphidae/Syrphidae_World_Phylogeny.htm) project.

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Project

This PhD project is under development by [Trevor O. Burt](#) at the ZFMK (Diptera Section) in Bonn, Germany under the supervision of [Ximo Mengual](#) (ZFMK, Centre of Taxonomy and Evolutionary Research) and [Bernhard Misof](#) of Rheinische Friedrich-Wilhelms-Universität Bonn and ZFMK (Centre for Molecular Biodiversity Research). This PhD project is one of fifteen research areas within the [BIG4 EU Consortium \(Biosystematics, Informatics and Genomics of the 4 big insect Orders\)](#), and will be submitted as a doctoral dissertation in partial requirement in the completion of a Doctoral Program in Biology at the University of Bonn. Upon successful defense Trevor O. Burt will receive the title of Doctor of Biology.

Grant title

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Hosting institution

Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; Rheinische Friedrich-Wilhelms-Universität Bonn, Germany; and various collaborators and partners.

Author contributions

Trevor O. Burt wrote the main body of text. Ximo Mengual edited and revised the manuscript. Ximo Mengual developed the initial research question and concept of this PhD project, which were refined with the doctoral candidate, Trevor O. Burt.

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