# Integrative taxonomy of araneomorph spiders: Breathing new life into an old science

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# Chapter 1

# General Introduction

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# Taxonomy: what it is, what are its problems and the proposed solutions

Taxonomy is the science and practice of the classification and description of things; in biology, it encompasses the description, identification, nomenclature, and classification of organisms based on their inferred relationships [1–3]; this is the general notion of what taxonomy is and what a taxonomist does. However, in the context of biology, taxonomy has a much broader background that involves all sort of biological knowledge, from the formal naming of groups of organisms (e.g. species) to the temporal and spatial distributions of those groups, their morphology, anatomy, behavior, molecular information, among many other data. The science of taxonomy is currently in a state of transition, where content within publications is being digitally mobilized and incorporated into an interconnected knowledge network.

Throughout its more than two centuries of existence, taxonomy has provided a nomenclatural and relational framework to all the biological disciplines setting the foundations for discovering and understanding biodiversity. Nevertheless, this foundational role can often be confounded with a trivial and expendable one, or even be considered as a mere "service provider" [4, 5] to other fields of science. This perception of simplicity in the taxonomic endeavor, together with the realization of the massive number of undescribed —and unknown— taxa [6–12] and the human impact imposed on ecosystems lead to a crisis commonly known as the *taxonomic impediment* [6, 8, 13–15].

This taxonomic impediment (or impediments?) has become symptomatic in many ways, namely: the reduction of the taxonomic workforce and university curricula; the reduction of funding and economic support; and the view of taxonomy as an obsolete science [4, 9, 14–22]. An unintended consequence has also been the reduction in the literature outlets, leaving fewer venues for the publication of fundamental science. This problem has been highlighted by the recent decision to exclude the taxonomic mega-journal Zootaxa from widely used science evaluation metrics (although this decision was subsequently reversed in the wake of reactions from the taxonomic community) [23–25].

This taxonomic impediment was noted by governments during the late 1990's and some agencies like the American National Science Foundation (NSF) created programs to enhance taxonomic training and research for future generations. That was the case of the Partnership for Enhancing Expertise in Taxonomy (PEET) [14, 26–28]. Similar projects were created in other countries like a federal directive for training specialists in cladistics in Brazil [19] and the Darwin Initiative in the UK. These programs looked to revive taxonomy, increase the workforce (especially in little known and neglected taxa), and stimulate the production and sharing of information on the internet, making taxonomic knowledge more accessible. A survey of the PEET impact in the creation of

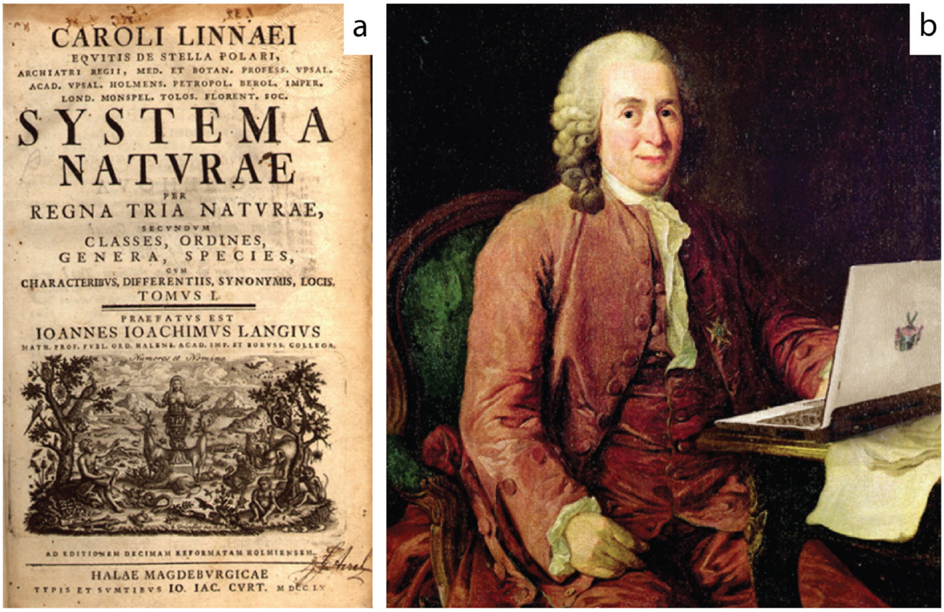

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**Figure 1.1.**-“***Linnaeus in the information age***”. a) The tenth edition of Carl Linnaeus’ *Systema Naturae* published in 1758. Modified from Pyle [43]. b) Depicts an anachronistic portrait of Linnaeus —considered the father of Taxonomy— as a *techie*, using modern technology to develop his science. Modified from Godfray [5].

taxonomic careers showed that although PEET trainees greatly impacted scientific production in their respective fields, there were common concerns about funding continuity and the opportunity of finding steady jobs in taxonomy [28]. This same work emphasized the need for multidisciplinary training that, in addition to traditional taxonomic skills, also developed competence in the use of molecular techniques, data management, information dissemination, etc., as well as capabilities for integrating taxonomy with biogeography, ecology, ethology, etc.

It is clear then that taxonomy needs to change to improve taxonomy-based products and keep up with modern, faster data-driven science. Essential elements for 21st century taxonomy include universal access to primary source information [29–31] and the incorporation of new technologies to facilitate better description, analysis, understanding and conservation of biodiversity (Fig. 1.1). In this context, Godfray and Knapp [17] summarized the major changes that taxonomy has gone through in recent decades, transforming from a purely descriptive discipline to a hypothesis-driven science. This transition has been driven by a “philosophical makeover” that incorporated phylogenetic systematic ideas to test relationships between taxa, along with advances in DNA sequencing that have made vast amounts of molecular data available. Similarly, Godfray [5, 30] and Wheeler et al. [15] have articulated the need to build a more robust online taxonomic infrastructure to overcome some common problems in taxonomy, such as the publication of isolated descriptions, and limitations in data and image sharing and publication. The first decade of this century saw a healthy and necessary debate concerning the significance of taxonomy, its role among the modern biological science, and the epistemological, philosophical and technical reforms needed for taxonomy to stay relevant in the future [5, 8, 9, 15, 17, 18, 20, 21, 29, 30, 32–42]

## *"Taxonomy as a team sport"*

Taxonomy is often understood as the individual efforts of taxonomists working in isolation; however, the current state of taxonomic science and the pace of the loss of biodiversity demand taxonomy become a group effort that greatly takes advantage of the internet and its capabilities to accelerate the rate and quality of its production and distribution [35]. The taxonomy of a group of organisms typically arises from the growing collection of publications in the primary taxonomic literature of that taxon, and does not reside in a single publication or institution. As such, it tends to be scattered among multiple journals, with contributions by various authors; this has made taxonomic literature a (usually) poorly defined integral of the accumulation of literature [30] with a tendency to be unorganized and fragmentary. Godfray [30] suggested the implementation of a unitary model of taxonomy where one group or institution would be in charge of the administration of current taxonomy for a given group. Spider taxonomy, together with a few other examples like ants [44, 45], lepidopterans [46], dipterans [47], orthopterans [48] and fishes [49], are probably the finest working examples of this authoritative "unitary taxonomy" [30, 31, 50] model.

The taxonomy of spiders is probably one of the best curated and polished, being under constant revision since the mid-20th century, and currently being administered by the World Spider Catalog [51]. The indexation and scrutiny of spider taxonomic literature began in the 1940's by Pierre Bonnet (University of Toulouse, France) and Carl Friedrich Roewer (Bremen, Germany). Afterwards, the Italian arachnologist Paolo M. Brignoli (University of Aquila, Italy) started filling the gaps in the aforementioned works and publishing periodic catalog supplements. This idea was subsequently picked up by the American arachnologist Norman I. Platnick (American Museum of Natural History, New York) who published three catalog supplements between 1989 and 1998 [52–54]. After this, the online version of the World Spider Catalog (WSC) was established and handled by Platnick from 2000 to 2014 [55]. In 2014, the WSC was transformed into a relational database administered by the Natural History Museum Bern (Switzerland) [51]. This catalog provides a fully searchable database that grants access to information on the more than 48,700 currently valid spider species and their synonyms. The WSC website also keeps a fully accessible library with more than 15,400 documents on spider taxonomy that dates back from the current year to Carl Clerck's species descriptions from 1757, the only accepted spider descriptions previous to the Linnean era (ICZN: Article 3.1) [56, 57].

## Improving access, dissemination and usability of information

Economics is the study of the production, distribution, and consumption of goods and services. If the scientific community is working to modernize the production, distribution, and consumption of taxonomic information, then perhaps we should look to economics for guidance. But economics is dominated by the study of physical goods, whose value is largely driven by their scarcity: rare things tend to be more valuable than common things. In contrast to physical goods information becomes more valuable as it becomes more accessible. So to increase the value of taxonomy, we should work to increase accessibility to biodiversity knowledge [58]. Current technologies allow storing and sharing data at an unprecedented pace, which in turn, allows the transformation of old printed literature (e. g. the Biodiversity Heritage Library [59]), and direct publication of new literature in electronic PDF format. This permits world-wide access to an amount of knowledge that was previously reserved to a few great libraries [15], recovering centuries of aggregated data that might otherwise just be forsaken on a library book shelf or at the back of a researcher's drawer. Nevertheless, it is not the best format for exchanging and querying data generating what has been dubbed the " PDF Black Box" [60]. In this context, the Swiss organization Plazi [61] has created software that semiautomatically detects and extracts taxonomic treatments, pieces of text that link specimen data (e.g. collection locality and date, collector, number of specimens, developmental stage, among others) to a taxon name [62–64].

The Plazi initiative [65–67] has greatly benefited from electronic access to taxonomic literature in PDF format and has focused on mining and mobilizing biodiversity and taxonomic data contained in legacy and newly produced taxonomic literature. This can be done in two ways: a retrospective approach that transforms a taxonomic document in PDF format into a sematically categorized document in XML format that allows specimen data to be extracted; and a prospective approach where data is directly produced in XML format as has been implemented by some journals (e. g. Pensoft's ZooKeys and Biodiversity Data Journal, the European Journal of Taxonomy, among others) [58] (Fig. 1.2). These taxonomic treatments are then stored and available in Plazi's Treatment Bank where the specimen data can be directly gathered and analyzed [68]. Also, a main characteristic of this repository is that these specimen records are also contributed to the Global Biodiversity Information Facility [69], where they are aggregated with other sources of data such as collection specimen records and observations networks (among other sources), forming an unparalleled resource for discovering, analyzing and explaining broad biodiversity patterns [63–65, 68].

In this thesis, we explored the application of these principals in **Chapter 2**, focusing on the extraction of data from legacy taxonomic literature and its application for inferring

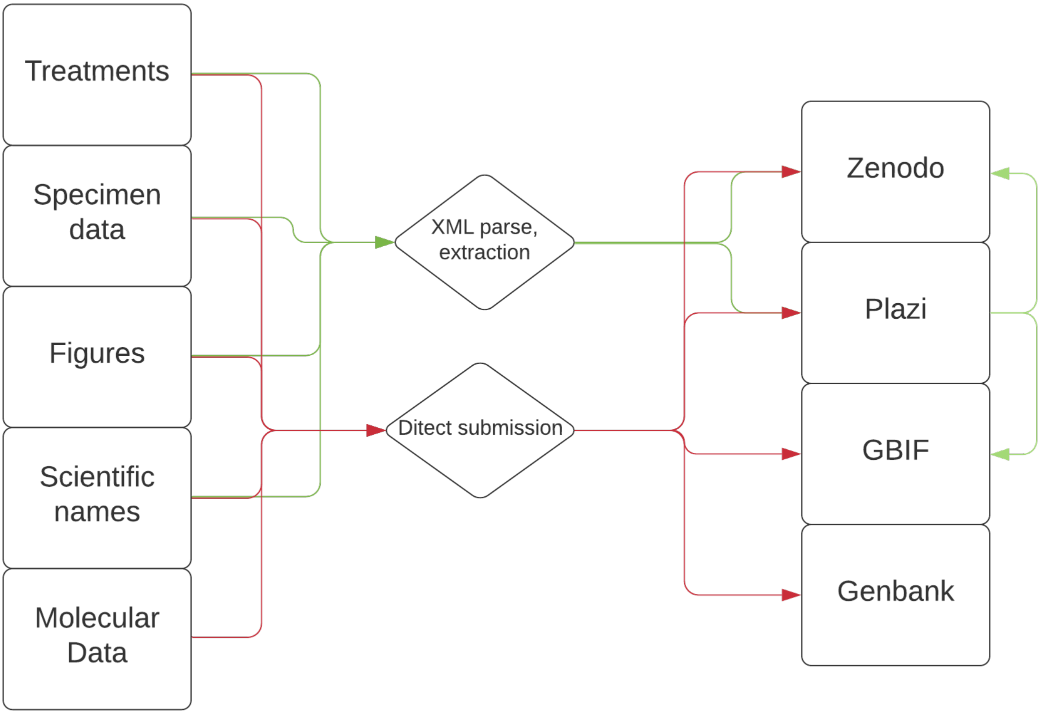


**Figure 1.2.-The "Plazi approach".** Schematic view of the retrospective (green) and prospective (red) data mining from taxonomic literature. Extracted data can then be displayed and analyzed in specialized repositories [61, 70] and databases [61, 69, 71].

phenological patterns that allow optimizing specimen sampling in the field (see also the fieldwork section below). Also, we used taxonomic literature obtained from the WSC to assess the rare phenomenon of genital asymmetry (GA) in spiders (**Chapter 3**, see the *Teutamus politus* section below). This chapter used taxonomic literature as an image repository observing and comparing the incidence and biological background of GA, giving a hypothetical classification based on previous work in spiders and insects GA [72–80] and drawing a preliminary evolutionary scenario for each type of asymmetry we observed [81].

## The integrative taxonomy

Integrative Taxonomy was defined by Dayrat [4] as the complementary delimitation of species based on their phylogeography, morphology, genetics, ecology, behavior, etc. Although the term, as minted by Dayrat [4] failed to be the proposed "new paradigm" in the exercise and understanding of the taxonomic science and was even dubbed as potentially misleading and detrimental by Valdecasas et al. [82] due to its *guidelines* on the taxonomic nomenclature, there are some concepts that are worth recovering

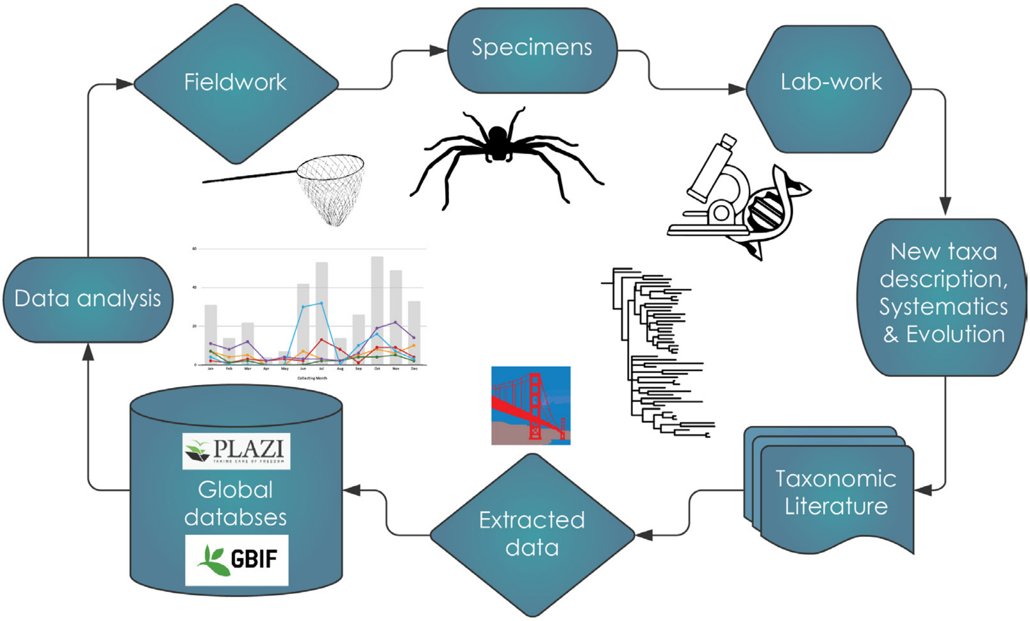


**Figure 1.3.- The integrative taxonomic pipeline.** Schematic workflow of the taxonomic process used in this thesis. It includes the use of the WSC [51] as a taxonomic library; the extraction of data from taxonomic literature [65, 66]; the use of these and other specimen data for biodiversity analyses; the use of molecular data (some of it from Genbank [71]) for building the phylogenies and a thorough documentation with different imaging techniques of the specimens' morphology.

and incorporating, whenever possible, in the common practice of taxonomy. Taxonomy has generally entrusted this species delimitation on morphology due to both practical and historical reasons. Nevertheless, as mentioned before, the current taxonomic crisis requires the inclusion of new technologies and techniques that favor faster and more reliable taxa descriptions; integration means multidisciplinarity [4, 83].

This multidisciplinarity has become more and more common in some fields by the integration of: morphological data (e.g. photographs, SEM, 3D imaging, CT-scans, geometric morphometrics, among others), molecular data, geographical information (e.g. collection localities and the use of GIS), and other specimen based data (e.g. number and sex of specimens, collection dates, etc.) that allow testing the species hypotheses in different and more robust approaches [4, 82, 84–86]. Pyle [43] visually exemplifies the enormous advances on species documentation by using these modern technologies. The integrative perspective, besides generating pure taxonomic information —hypotheses of classification and relations—, also contributes with molecular data, high resolution images of specimens and their relevant characters, and other kinds of data to global databases [86–92]. This accessible data can be downloaded and tested independently or incorporated to new taxonomic and systematic studies in an easy and flexible way; this can help to expedite the testing of phylogenetic hypotheses and rapidly generate new datasets and inferences with more explanatory power.

In this context, **Chapters 4** and **5** are examples of the implementation of this integrative taxonomy (Fig. 1.3). Both chapters involve the description of new taxa and also, first reports of these families for Thailand. **Chapter 4** describes two new species and one new genus of the family Hahniidae based on molecular and morphological evidence; **Chapter 5** describes three new species of the family Symphytognathidae, employing molecular and morphological evidence; and making use of micro CT-scans and 3D modeling to circumscribe the genus *Crassignatha* and clearly illustrate and discuss the genital characters of the males of this and other related symphytognathid genera. Although 3D modeling had been used before to study spider genitalia [93–95], ours are, to the best of our knowledge, the smallest spider palps that have ever been 3D modeled, being only 0.2 mm in width.

## Fieldwork

The process of how we selected the locations where fieldwork was conducted is explained in detail in **Chapter 2**. Here we cover some generalities of the new specimen collection, where and how it was conducted. Southeast Asia (SEA) is one of the most diverse areas on the planet being represented by several conservation hotspots, of which the Indo-Burma and the Sundaland Hotspots are the most extensive and diverse [96, 97] (Fig. 1.4). The Indo-Burma hotspot is largely distributed over continental SEA; this region is characterized by socio-political instability, high population density and a fragmentary nature of its territory. This, in turn, generates a scattered taxonomy of most groups that makes it difficult to describe and assess its biodiversity [96, 98, 99]. Still, studies on vascular plants and terrestrial vertebrates show the Indo-Burma hotspot to be one of the richest and highest in endemism, but also one of the most threatened hotspots [96, 100].

This uniqueness and magnitude of its biodiversity is also reflected, albeit understudied, in invertebrates. The arachnofauna is mostly known from isolated species descriptions, although a few genus, family and broader revisions have been published [101–103]. Especially interesting to us was the case of the liocranid spiders, and from this family, the species *Teutamus politus* Thorell, 1890 (see *T. politus* section below, and **Chapters 2** and **3**) and its close relatives in the so called *Teutamus* group (TG). While planning our fieldwork, we wanted to improve the probabilities of capturing adult specimens of *T. politus* while also sampling other relatives of the TG. Due to the lack of data on these spiders' phenology, we used data from taxonomic literature to select the localities and times with a higher incidence of liocranid spiders based on the number of adults reported in taxonomic literature. Taking into account this information we decided to collect from July to August 2018 in the three provinces with most specimens reported in Thailand. We covered a variety of habitats in each place (Fig. 1.5) ranging from cloud forests at the top of the highest mountain in the country, to temperate pine, oak and *Dipterocarpus* forests down to tropical vegetations. We also sampled in secondary forests and rubber and oil palm plantation to observe the anthropogenic impact on the populations of these spiders.

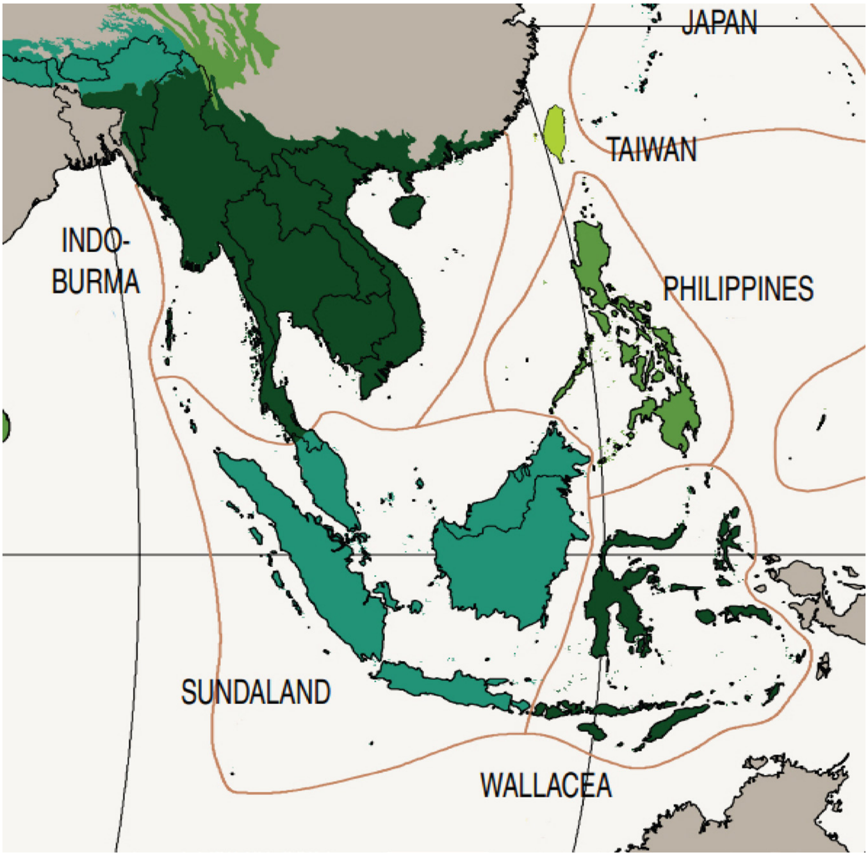
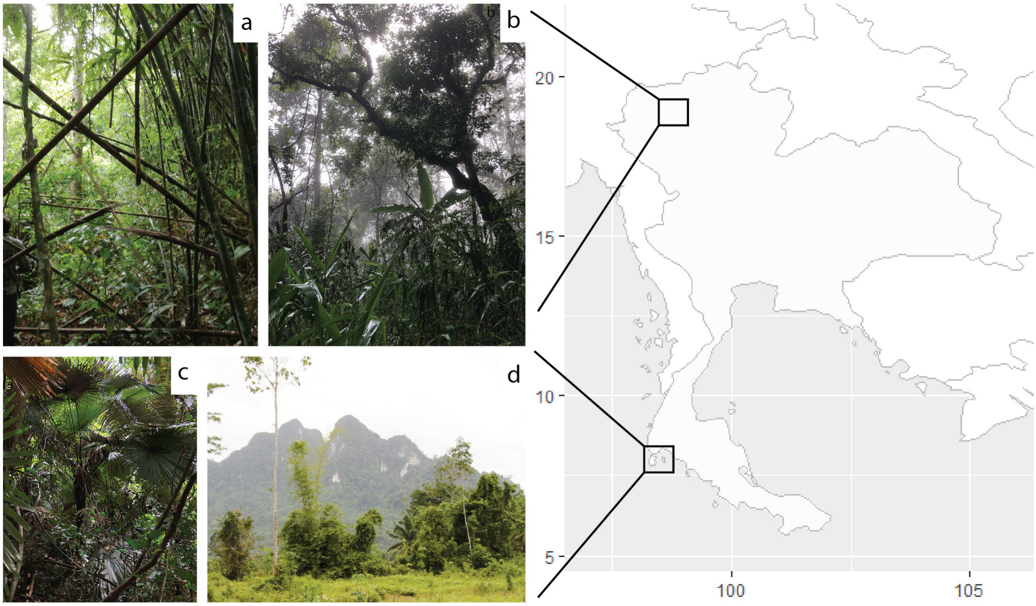


**Figure 1.4.-Map of the Southeast Asian Hotspots.** Modified from Mittermeier et al. [96].

**Figure 1.5.- Some of the localities sampled in Thailand.** a, b) Chiang Mai: a- bamboo forest in the Pha Daeng National Park. b- Cloud forest in Doi Inthanon National Park, the highest mountain in the country. c, d) Phuket and Krabi: c- a patch of *Kerrodoxia elegans* palm tree in Ton Sai. d. Secondary forest near Than Bok Khorani National Park. (Next page, top) ►

**Figure 1.6.- Collecting methods.** a) Winkler traps hung outside Doi Suthep National Park headquarters. b, c) Pitfall traps at a *Dipterocarpus* sp. forest near Pha Daeng National Park. d) Active search in sifted leaf litter at Doi Suthep National Park. e) Active search in cryptic habitats (i. e. under rocks, logs, bark, among leaf litter, etc) near Than Bok Khorani National Park. (Next page, bottom) ►

Also, we knew based on literature that most liocranid adult specimens were collected using pitfall traps and leaf litter sifting [101, 103–105]. Therefore, we used a combination of collecting methods (Fig. 1.6) that target ground spiders [106–108]. This allowed us to have a better representation of the liocranid species present in each site and also to capture a wide array of ground dwelling arthropods, including several families of spiders. While referring to records in taxonomic literature when planning field work is a common practice, very few have made such records persistently available to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all using FAIR [67, 109] standards in the way we did for the present work. More information about this fieldwork, data extraction and applications can be found in **Chapter 2** of this thesis. Specimens collected during this field trip were used to observe and document the genital asymmetries in *T. politus* (**Chapter 3**), and to describe new species and build molecular phylogenies of the families Hahniidae and Symphytognathidae (**Chapters 4 and 5**).

## *Teutamus politus*

Fig. 1.7

This species is a central part of this thesis, together with other related taxa of the *Teutamus* group, of the Chapters 2 and 3.Very little is known about the biology of this interesting species. It was first described in 1890 as the type species for the genus *Teutamus*. Its description was based on one female specimen from “Pulo Pinang”, nowadays Malaysia [110]. But it wasn’t until 2001 that their name resurfaced among many others in an impressive piece of taxonomic literature on South East Asian ground spiders by the Dutch arachnologist Christa Deeleman-Reinhold [101]. This seminal work encouraged research on this and other related spider groups in the region [103–105, 111–113]. Deeleman-Reinhold [101] described six new species of this genus, observing relevant information about the habitat and distribution of these species. She made the first description of the male of *T. politus* and noted the asymmetric genital opening in the female. Dankittipakul et al. [104] significantly increased the knowledge of the genus *Teutamus* by describing 17 new species. They reported many new specimens of *T. politus* increasing the available information about their geographic and temporal distribution. These studies greatly advanced knowledge about the taxonomy, and geographical distribution of *T. politus* and other related spiders. However, their biology is still a mystery.

*Teutamus* species are known to inhabit the leaf litter of dark humid undisturbed rainforests, but have also been reported wandering on the forest floor in daytime. Most species were found to have limited distribution ranges, being sampled in just one locality without known overlapping distributions [101]. *T. politus* is the notable exception by having a relatively wider distribution that extends from Malaysia to the south of Thailand [101, 104].This species became interesting to us due to the clearly asymmetric female genitalia. This character had been noted and illustrated before (Fig. 1.7d) in the female and had even been used as a diagnostic character of the species but correlations to changes in male morphology and other implications like courtship and mating behavior (Fig. 1.1c) had never been studied. More information about this can be found in the third chapter of this thesis. While sampling specimens of this species our attention was

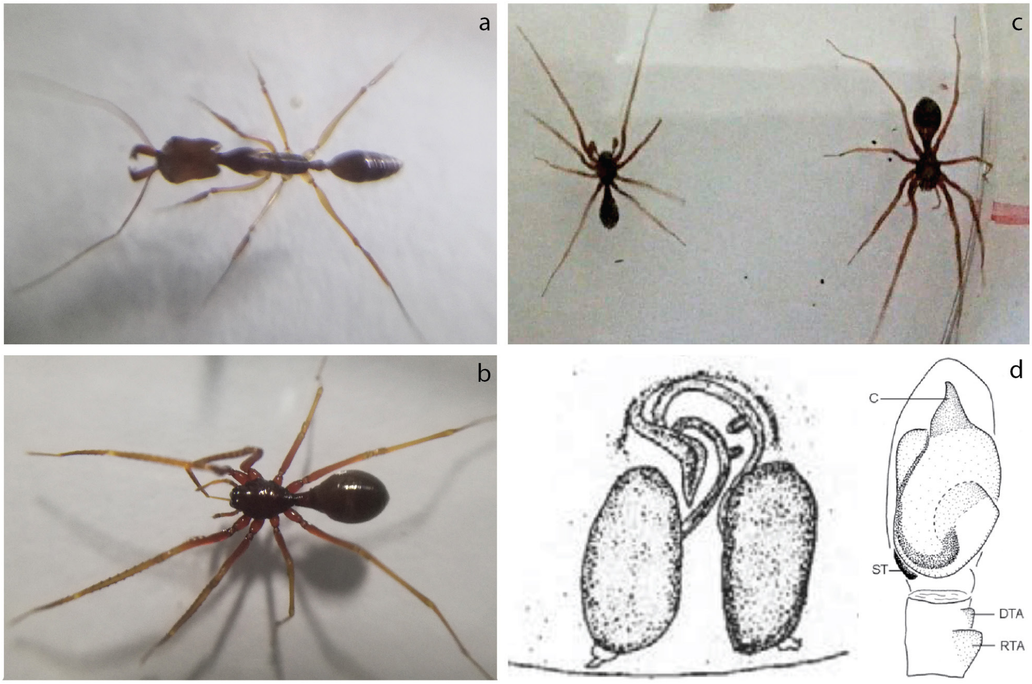

**Figure 1.7.**- ***Teutamus politus.*** a, b) Comparision of an ant *Odontomachus* sp. and a female of *T. politus*; exemplifies the phenomenon of ant mimicry in this spider species. Our sampling also showed them to be myrmecophylic, living on top or close to the *Odontomachus* sp. nests. c) Size comparison of male and female during the behavioral experiments. d) Taxonomic illustrations of the genitalia of this species (female epigynum —left—, and male pedipalp —right—). Modified from Deeleman-Reinhold [101]; and Dankittipakul et al. [104].

drawn to the relation they had with ants of the genus *Odontomachus* (Fig 7a). Most of the *T. politus* specimens we caught were close to or on top of these ant nests. *T. politus* bears some morphological similarities to the ants (Figs. 1.7a, b). Although they had been mentioned to be “vaguely ant-mimicking” before [101], this is the first time that this kind of spider-ant relationship has been observed in this genus. Unfortunately we were not able to make more detailed observations of the nature of the relationship. Nevertheless, similar interactions have been well documented in other spiders ranging from *myrmecophyly* —living in close relation to ants— to *myrmecomorphy* —morphologically mimicking the ants— [114–118].

The present thesis aims to show the value of generating new taxonomic content in a way that allows for rigorous testing of phylogenetic hypotheses, and boosts the impact and relevance of taxonomic work by incorporating high resolution images, molecules and specimen data. Although taxonomy is a venerable science, it holds large quantities of useful data that can help elucidate broad patterns in biological evolution, biogeography, and ecology, among other disciplines. All of these might eventually help understanding, protecting and preserving our endangered biodiversity. We are sitting on a mine whose precious data patiently awaits to be extracted.

# Thesis outline

## Legacy literature data extraction and application

**Chapter 2:** Mining data from legacy taxonomic literature and application for sampling spiders of the *Teutamus* group (Araneae; Liocranidae) in Southeast Asia. *Scientific Reports* 10, 15787. doi:10.1038/s41598-020-72549-8.

## The use of taxonomic literature to infer evolutionary patterns

**Chapter 3:** Imperfect and askew: A review of asymmetric genitalia in araneomorph spiders (Araneae: Araneomorphae). *PLoS One* 15:6, e0220354: 1-26. doi:10.1371/journal.pone.0220354.

## New taxa description in an integrative approach

**Chapter 4:** First records and a new genus of Comb-tailed spiders (Araneae: Hahniidae) from Thailand with comments on the six-eyed species of this family. *European Journal of Taxonomy* 724, 51-69. doi: 10.5852/ejt.2020.724.1157

**Chapter 5:** First records and three new species of the family Symphytognathidae (Arachnida: Araneae) from Thailand, and the circumscription of the genus *Crassignatha* Wunderlich, 1995. *ZooKeys* 1012, 21–53. doi.org/10.3897/zookeys.1012.57047

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