Reconstructing the Tree of Life

Taxonomy and Systematics of Species Rich Taxa

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13 Insect Biodiversity and Industrialising the Taxonomic Process: The Plant Bug Case Study (Insecta: Heteroptera: Miridae)

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ABSTRACT

Insects are the most diverse higher taxon of organisms, comprising more than half of all described species. The rate and scale of species extinction and ecosystem degradation, the so called biodiversity crisis, demands an urgent response by the taxonomic community to comprehensively document global organismal diversity. For 'megadiverse families' within insects, the establishment of predictive classifications that are global in scope and the description of 'all species' are hampered by the scale of the task. To answer this challenge, we support previous calls for industrialising the taxonomic process, involving astronomy-like international collaboration, infrastructural investment, capacity building and taking full advantage of information technology developments. We strongly argue that this unitary approach can be implemented without compromising the hypothesis-driven nature of taxonomic science. The plant bug family Miridae is presented as a case study of this approach.

13.1 INTRODUCTION

If we could visualise a tree of life, insects would form the canopy, overshadowing the rest of life (Figure 13.1; insects are the major component of Hexapoda). Nearly a million species of insects make up the 1.7 million species of organisms so far described. Despite their omnipresence, insects are not a recent explosive radiation, nor mere variations on a theme. Insects have a minimum history of 400 million years, and most modern insect orders have been in existence for around 250 million years[1]. Insects are the most dominant and diverse group of terrestrial metazoans by almost all possible measures. Aside from submerged marine habitats, there are few ecological niches that insects have not exploited. In terms of abundance and biomass, insects dominate most terrestrial ecosystems. For instance, arthropods (primarily insects) reach extraordinary biomasses (23.6 kilograms per hectare) and abundances (23.9 million individuals per hectare) in Borneo[2]. Termites alone can reach abundances of up to 10,000 individuals per metre squared[3] and biomasses of 100 g per metre squared[4]. Insects are crucial to terrestrial ecosystem processes such as nutrient cycling[5], seed dispersal[6] and pollination[7].

By virtue of scale alone, no other group epitomises the challenges that species rich taxa present to taxonomy and systematics quite like the insects do. How many of the 350,000 described beetles does one include when reconstructing the phylogeny of Holometabola? How do we reduce duplication of effort so that we do not repeat historic levels of up to 80%[8] synonymy within the Insecta? How do we describe the four to nine million undescribed insects (Table 13.2) within a time frame that meets the demands of scientifically informing the biodiversity crisis?

It is with the biodiversity crisis in mind that taxonomists and the taxonomic method are increasingly faced with questions about relevance. In this chapter we outline the issues that face entomologists in documenting this remarkable diversity of insects. We present the case study of plant bugs (Insecta: Heteroptera: Miridae) as a model group for preserving the taxonomic method but incorporating advances in technology and global cooperation as a means to expediting the documentation process.

13.2 ESTIMATES AND DRIVERS OF INSECT DIVERSITY

13.2.1 INSECT DIVERSITY AND CLASSIFICATION

Insects are the most species rich class in Arthropoda, a phylum of considerable diversity even without Insecta included. The vast number of insects and other arthropods suggests that the combination of an exoskeleton, a segmented body plan and jointed appendages have been a recipe for zoological success. The phylogenetic position of the insects within Arthropoda is
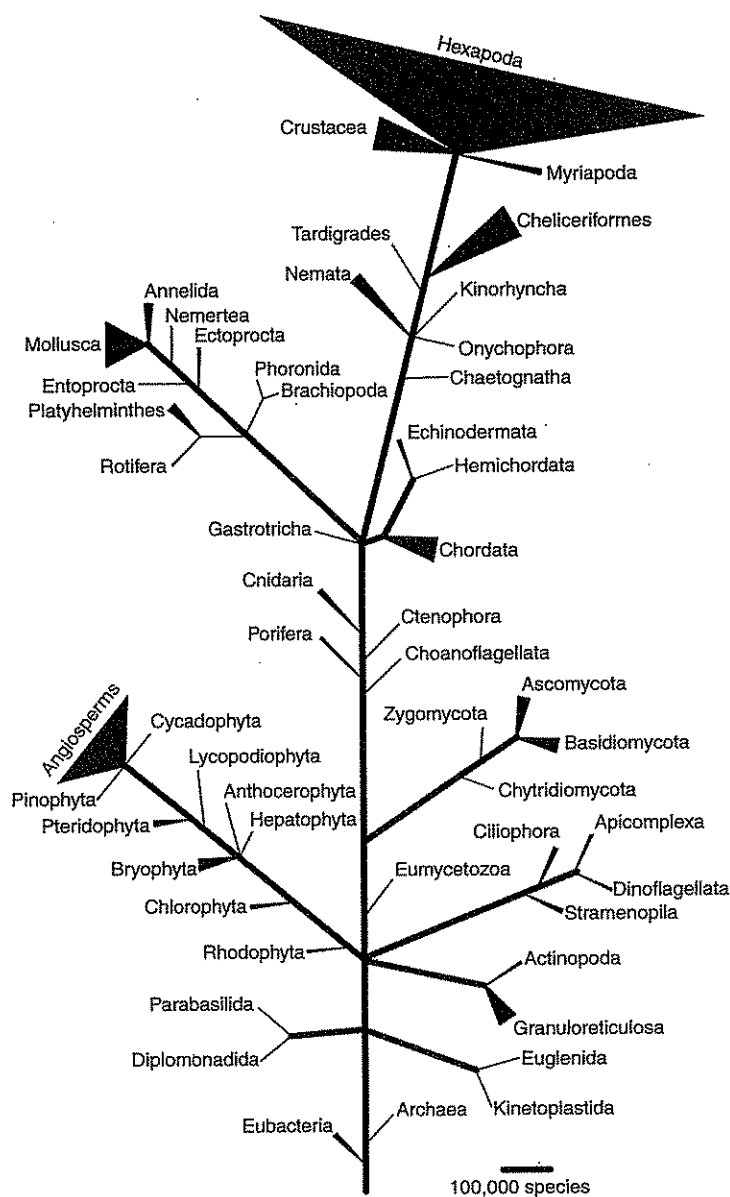
FIGURE 13.1 Tree of life with terminal branches expanded to represent number of described species in each taxon. Hexapods include insects, springtails, diplurans and proturans. (Tree structure is based on Pennisi[64] and taxon species richness estimates are from Brusca and Brusca[65], Margulis and Schwartz[66] and DSMZ[67].)

contentious, but has mostly come down to arguments about where the root of the phylogenetic tree lies. Most contemporary analyses that include DNA sequence data suggest that insects have arisen from within a paraphyletic Crustacea[9–11], although some authors have suggested that Hexapoda and Crustacea are mutually paraphyletic[12,13]. Within Insecta, interordinal relationships (Figure 13.2) are in some ways poorly resolved, although a great deal of progress has been made in the last quarter of a century. While some clades, such as Holometabola (Figure 13.2), have been well supported since before the time of Hennig, other problematic taxa such as Plecoptera have caused considerable instability in the deep level branching of insect phylogenetic reconstructions.

FIGURE 13.2 Interordinal phylogenetic tree of Hexapoda. Geological time scale is indicated on the left side. Wide branches indicate robust support in contemporary analyses.

The insect phylogenetic tree presented here (Figure 13.2) is a summary tree of recent work[14-16] in the field.

Approximately 925,000 described species[1] are represented in just 32 orders of insects, a tractable higher classification when compared to the approximately 100 orders of vertebrates. Yet, species diversity in the insects is dramatically uneven in distribution. The majority of species are found in just five orders (Table 13.1). Four of these orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera) belong to Holometabola, a clade characterised by development via complete metamorphosis (Figure 13.2). Together with Hemiptera, these orders represent close to 90% (c. 825,000 species) of the described insect diversity. This uneven distribution of described species diversity extends to every taxonomic level. In fact, just 20 families (Table 13.1) of insects contain a little over 45% of all described insect diversity. Most of these hyperdiverse families are primarily herbivorous, such as Chyrsomelidae, Miridae and Noctuidae, with some notable predaceous (for example, Staphylinidae) and parasitic (for example, Ichneumonidae and Tachinidae) exceptions.

TABLE 13.1
Described Species Diversity within the Hexapods

Order	Family	Species	Order	Species
Coleoptera		350,000	Orthoptera	20,000
	Curculionidae[68]	50,000	Trichoptera	11,000
	Staphylinidae[69]	47,000	Collembola	9,000
	Cerambycidae[68]	35,000	Neuroptera	6,500
	Chrysomelidae[68]	35,000	Odonata	5,500
	Carabidae[68]	30,000	Thysanoptera	5,000
	Scarabaeidae[68]	25,000	Phthiraptera	4,900
	Tenebrionidae[68]	18,000	Psocoptera	4,400
	Buprestidae[68]	15,000	Blattodea	4,000
			Ephemeroptera	3,100
Lepidoptera		150,000	Phasmatodea	3,000
	Noctuidae[70]	25,000	Isoptera	2,900
	Geometridae[70]	21,000	Siphonaptera	2,500
	Crambidae[70]	11,630	Dermaptera	2,000
	Arctiidae[70]	11,000	Plecoptera	2,000
			Mantodea	1,800
Diptera[71]		120,000	Diplura	1,000
	Tipulidae[71]	10,203	Protura	600
	Tachinidae[71]	9,451	Mecoptera	600
	Chironomidae[71]	7,739	Strepsiptera	550
			Archaeognatha	500
Hymenoptera		125,000	Embiidina	500
	Ichneumonidae[72]	15,000	Zygentoma	400
	Braconidae[72]	15,000	Zoraptera	32
	Formicidae[73]	11,839	Grylloblattodea	26
			Mantophasmatodea	14
Hemiptera		90,000		
	Cicadellidae[74]	20,000		
	Miridae[50]	10,040		

Note: Described species diversity within the hexapods. All orders and the 20 largest families are shown.

Source: Species richness estimates from Grimaldi and Engel[1] unless otherwise indicated.

13.2.2 DRIVERS OF DIVERSITY

The remarkable diversity found in Insecta has been attributed to several extrinsic and intrinsic drivers. Intrinsically, the development of certain 'key innovations' has been associated with increased rates of diversification within specific lineages of insects. Insects were the first animal lineage to evolve powered flight, and wings are considered to be one of their greatest morphological innovations. Specifically, the development of the wing flexion is associated with increased rates of diversification in Neoptera[17]. At a finer taxonomic scale, innovations such as pollen-collecting tentacles in yucca moths[18], and elongated snouts in weevils for preparation of oviposition sites[19] have been associated with species richness in those groups.

The coevolution of insects and plants is undoubtedly a key driver of diversity for many groups of insects. At the broadest scale, the explosion of insect diversity in the fossil record corresponds with evolution and diversification of seed plants[1]. More specifically, several studies[20,21] have shown that origins of angiosperm feeding within the beetles are associated with increased rates
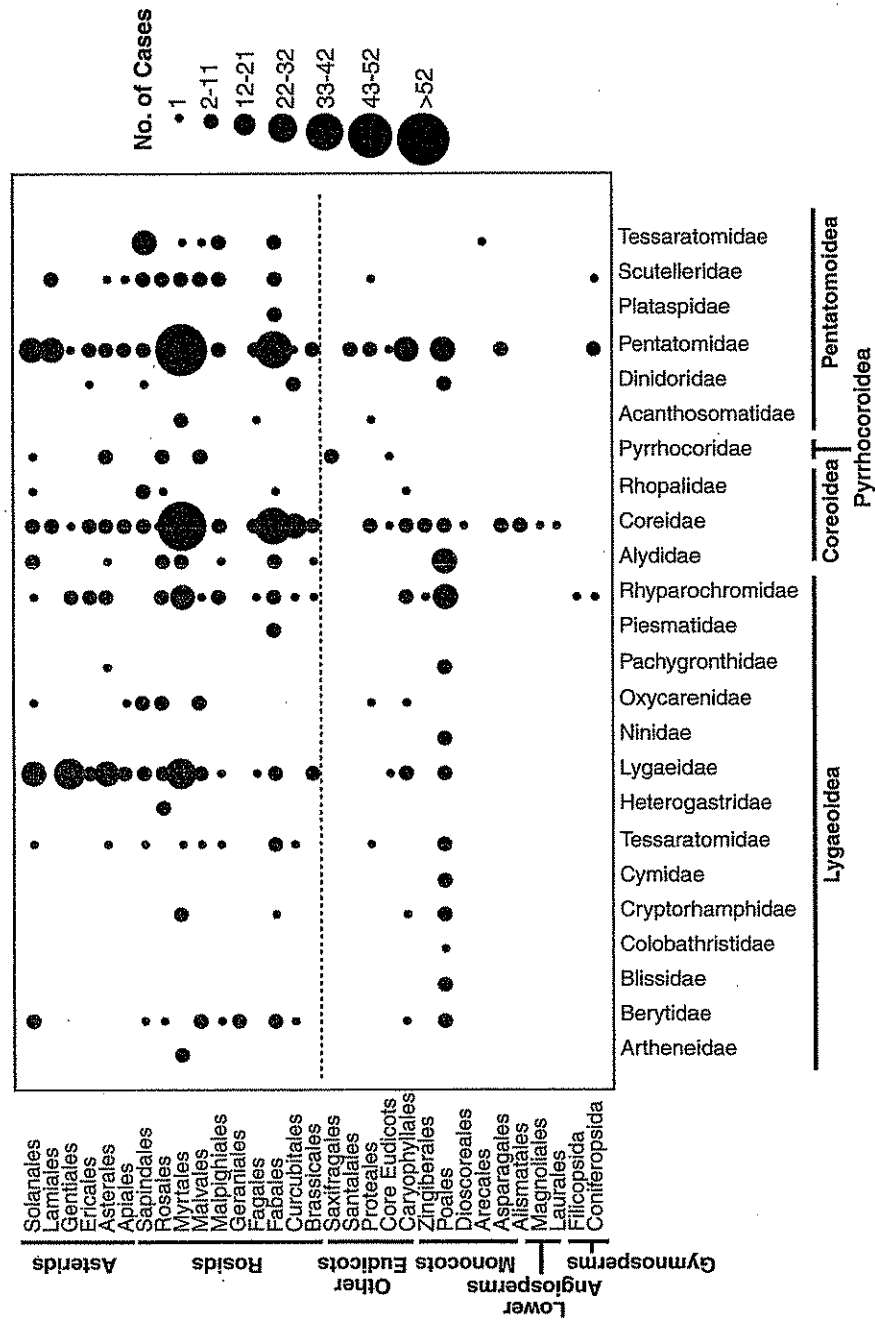
FIGURE 13.3 Host plant affinities of families of land bugs belonging to the infraorder Pentatomomorpha (Heteroptera) with ordinal taxa of land plants. Dashed line separates asterids and rosids from remainder of land plants.

speciation. Another example of insect/plant coradiation can be found within Australian Heteroptera. The landbug infraorder Pentatomomorpha is primarily phytophagous and associated with a broad range of vascular plants, but primarily flowering plants. The documentation of their hosts[22] reveals that the majority of Australian pentatomomorphans are associated with rosid and asterid angiosperms (Figure 13.3). Most extant pentatomomorphan families appear in the fossil record in the early Cenozoic[23], corresponding with increases in the dominance and diversification of rosid and asterid angiosperms[24,25]. Although there is a paucity of insect-plant cospeciation case studies (see Rønsted, *Chapter 9*), and stratigraphic correlations as proposed in the previous example are very coarse, the abundance of relationships between insects and plants is fundamental in explaining the adaptive radiation of insect herbivores.

13.2.3 ESTIMATES OF INSECT SPECIES RICHNESS

Understanding of the relationship of insects and plants has been central to developing estimates of global insect species richness. Contemporary debate over global insect species diversity began with Erwin's[26] estimation of about 30 million species of terrestrial arthropods globally. Erwin arrived at this figure by fogging a single species of tropical forest tree with insecticide; determining the number of species in the 'beetle rain'; estimating the number of host-specific beetles; multiplying this by the number of tropical tree species; and extrapolating to a total number of arthropods based on the known proportions of other arthropod groups relative to beetles. Many of Erwin's assumptions have been criticised in the literature[27,28], particularly his estimates of plant host specificity for insect herbivores. In fact, much of the variation we see in estimates of global insect species diversity (Table 13.2) can be attributed to variation in estimates of host specificity in insects[27,29-32].

Nonetheless, most contemporary authors agree on estimates of between 5 and 10 million species of insects (Table 13.2). But with the exception of an early conservative estimate by Hodkinson and Casson[33], the general trend has been that of decreasing estimates for insect species richness (Table 13.2). This trend, combined with high levels of synonymy in existing names in some groups[34,35], suggests that global insect species richness may be at the low end of 5–10 million species. However the pendulum may now be beginning to swing back towards higher estimates. Ødegaard[32], in a recent study incorporating phylogenetic relatedness, suggested a shift from the low end to the high end of the 5- to 10-million range[32]. Even higher estimates can be anticipated if DNA taxonomy or barcoding[36] and phylogenetic species concept[37] approaches take a more central role in species delineation (see Seberg and Petersen,

TABLE 13.2
Estimates of Insect Species Diversity in the Scientific Literature and the Year in Which They Were Published

Estimated Number of Species (in millions)	Reference	Year
30	Erwin[26]	1982
7–80	Stork[28]	1988
5	Gaston[75]	1991
1.8–2.6	Hodkinson and Casson[33]	1991
12.5	Hammond[76]	1992
5	Ødegaard et al.[27]	2000
2.0–3.4	Dolphin and Quicke[77]	2001
4–6	Novotny et al.[29]	2002
10	Ødegaard et al.[32]	2005

Chapter 3). For example, Agapow et al.[38] found a 48% increase in species names after phylogenetic revision and application of the phylogenetic species concept. In considering these adjustments, there is the potential for 7.4–14.8 million phylogenetically defined species of insects in the world.

Leaving all of these hypothetical assumptions, abstractions and extrapolations behind, there is a clear message in all of these estimates: insect taxonomists have a considerable job to meet the challenge of developing an encyclopedia of life[39]. In a survey of the Zoological Record from 2000 through 2004, we found an average of 8,500 new insect species described per year. At this rate, it will take 480 to 1,070 years to describe the world insect fauna (based on estimates of 5–10 million insect species). Clearly this rate of species description is not adequate in meeting the contemporary needs of society, including ameliorating the alarming decline in biodiversity. This rate must be multiplied by a factor of 10–24 in order to document scientifically the world's undescribed insect fauna in the next 100 years, and 100 times that if the fauna had to be described in the next 25 years, as some people have suggested.

13.3 DEALING WITH DIVERSITY: FROM THE COTTAGE TO THE FACTORY

The description of nearly one million insects in 250 years is not a meagre effort, but the issue of completing the task in a given time is compelling because of the universally recognised biodiversity crisis. The world is quickly approaching a sixth major extinction event[40], with species extinction vastly exceeding prehistorical rates[41]. In such an environment, the onus on completing biotic documentation is globally accepted, as evidenced by the development of international instruments and frameworks (such as the Convention on Biological Diversity and the Global Biodiversity Information Facility and Global Taxonomic Initiative) and funding schemes such as various US National Science Foundation programmes (for example, Partnerships for Enhancing Expertise in Taxonomy, Assembling the Tree of Life, Planetary Biodiversity Inventory), as well as the repeated call to arms[39,42,43] in the scientific literature.

The task, however, is not just a question of increasing resources and infrastructure, including arresting the alarming decline in training the next generation of taxonomists (see Schram, *Chapter 2*). Scientists such as Godfray[42] and Wheeler[43] have independently called for a 'new taxonomy,' where the process is global in scope, with emphasis on a new astronomy-like culture of cooperative research, while taking best advantage of information technology. Although there is not a consensus on a new methodology, amongst many taxonomic entomologists there is a tacit agreement that conventional, hypothesis-driven and morphologically based descriptive taxonomy remains at the core of the task. However, the question remains, if we retain a traditional taxonomic core, can international cooperation and computer technology alone increase the rate of species description by two orders of magnitude within a generation?

There are a number of other interlocking factors, such as classification and collection shortfalls (see Utteridge and de Kok, *Chapter 18*), that seriously impede the process of documenting all the species in nature. For taxa, such as the 'Big 20' families of insects, suprageneric classifications are often in contention and lack stability. For example, in the leaf beetles, family Chrysomelidae, there is polarisation in the suprageneric classifications being utilised, with some workers accepting the phylogenetic classification and recognition of 11 subfamilies of Reid[44], while others follow the previous, and more traditional classification[45], recognising 18 subfamilies. Likewise in the plant bug family Miridae, Schuh's[46] phylogenetic classification recognises 13 tribes, whereas the main alternative of Carvalho[47] lists 26 tribes, and some tribes in both classifications are placed in different subfamilies. This classificatory instability can result in uncertain species placement, increased rates of synonymy and the erection of many unnecessary monotypic taxa.

In addition, much has been made of the value of existing collections[48], but it is also clear that many cryptic groups of insects require specialised collecting. In the past 50 years there has been an ever increasing trend of taxonomists working on insect families rather than groups of families

or even orders. This has resulted in a concomitant change from general to specialised collecting. These new survey efforts have led to the discovery of large numbers of species that were not represented in existing collections. For example, in a recent revision[49] of Australian barkbugs (Aradidae: Mezirinae), 45 of the 93 species represented in Australia were described as new, based on material collected primarily by the revision's author.

In summary, if the intent is to describe all insects in nature, and not just those in existing collections, then the taxonomic impediment is not merely a shortfall in species description. Codependent classification and collection impediments require parallel attention. In the following sections we provide a case study that documents the methodological transition from the single investigator to an industrial model of taxonomy that strives to overcome taxonomic classification and collection impediments within the plant bug family Miridae.

13.4 PLANT BUG DIVERSITY, BIOLOGY AND CLASSIFICATION

The plant bugs, or family Miridae (Figure 13.4), are the most speciose family in the hemipteran suborder Heteroptera, with 1,507 genera and 10,040 species described[50]. This has long been considered to be an underestimate of the number of plant bugs worldwide. In fact, the number of species currently described is, at most, half of that to be found in nature[51]. This makes Miridae one of the most species rich families of organisms known (Table 13.1).

Although mirids are known colloquially as plant bugs, they exhibit broader ecological diversity than their common name would suggest. Numerous taxa are largely ground dwelling in their habits (for example, Cylapinae: *Vannius* complex[52]; Phylinae: Hallodapini). Likewise, though most species are phytophagous, a significant number of taxa are predaceous (for example, Isometopinae, Deraeocorinae: Termatophylini[53]), and information is gathering that numerous species are zoophytophagous (for example, Bryocorinae: Dicyphini[54]). The biology of the basal taxa is not well known, but it is apparent that members of Cylapinae, such as the type genus *Cylapus,* feed on fungal mycelia[55]. For the phytophagous plant bug species, there is accumulated evidence that the majority of species show a high degree of host specificity, with most restricted to a single host plant[56–58].

Divided into seven subfamilies, 75% of the diversity of plant bugs occurs in three subfamilies; Mirinae, Orthotylinae and Phylinae. Mirinae are the most diverse subfamily of plant bugs, with over 40% of all mirid species. However, Orthotylinae and Phylinae (Figure 13.5) together contain an equivalent number (35%). One of the more outstanding features of the Orthotylinae and Phylinae is the multiple evolutionary development of ant mimetic taxa (Figure 13.4A), with
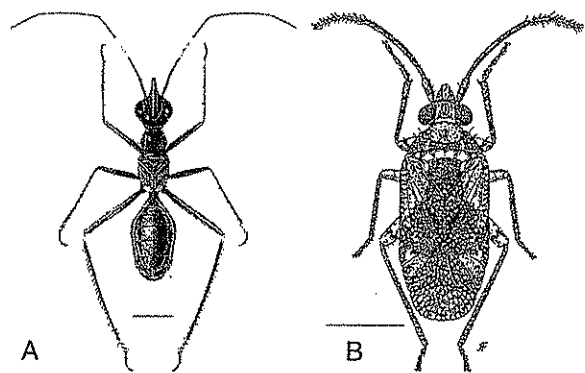

FIGURE 13.4 Two undescribed species of Miridae from Australia: *Mymecorides* sp. an ant mimic (A) and *Peritropis* sp. (B). Scale bars = 1 mm.
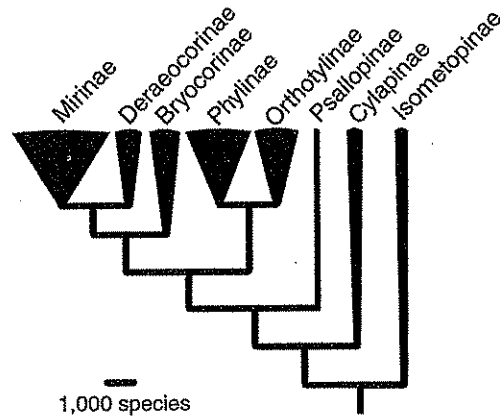
FIGURE 13.5 Phylogeny of Miridae with terminal branches expanded to represent number of described species in each taxon.

myrmecomorphy being found in hundreds of species and many genera. The majority of Orthotylinae and Phylinae is highly host specific, occurring primarily on meristematic growth of developing flowers and/or shoots.

13.5   PLANT BUGS AS A COTTAGE INDUSTRY

The taxonomic history of the group has modest beginnings, with Linnaeus[59] describing 17 species in 1758. A species description accumulation curve for Miridae subfamilies Orthotylinae and Phylinae (Figure 13.6) indicates that the description of world fauna was largely gradual until the last quarter of the nineteenth century. Around this time, numerous European scientists began describing new species from the Southern hemisphere, the Indian subcontinent and Central America. The twentieth century saw the increased saturation of species descriptions for the Nearctic and Palaearctic regions, as well as the continued enhancement of the plant bug faunas of Latin America and Africa. Plant bug alpha taxonomy was transformed between 1957 and 1960 when Carvalho
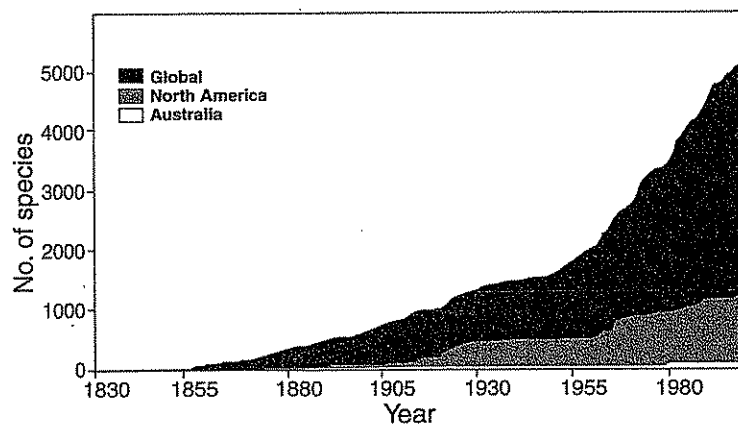

FIGURE 13.6 Global and regional chart of species description accumulation for the Orthyotylinae and Phylinae from 1830 to present.

published the multipart *Catalogue of the Miridae of the World*. An updated version of the catalogue was published in 1995 by Schuh[58], who now maintains an up-to-date online version[50]. Since Carvalho's catalogue, species have been described at a rate of approximately 145 species per year. This represents a doubling of the rate of the previous 50 years (73 species per year) to the publication of the catalogue.

Plant bug taxonomy has historically been a cottage industry in which single investigators have worked on regional collections, producing a modest list of species names over a lifetime. In total, some 340 authors (excluding junior authors) have published 13,048 species group names in Miridae. Although synthetic 'global' taxonomists have emerged throughout history, the vast majority of plant bug taxonomists (73%) have described fewer than 15 species. Until recently, most plant bug taxonomists worked alone. Only 13% of plant bug names are described in multi-author papers, suggesting that the image of taxonomists as lone investigators working in isolation is an apt description of past behaviour. However, when these data are partitioned by decade of description, a different image emerges. Since the 1970s, the proportion of plant bug species described in multi-authored papers has steadily increased by an average of 5% a decade. In fact, in the last ten years, 40% of plant bug species names are the product of a collaborative effort.

What are the benefits of collaborative efforts? Collaboration almost invariably increases taxonomic and/or geographic breadth. In particular the collaboration of global authorities with regional experts reduces redescription of geographically widespread species. For example, Carvalho, the most prolific global plant bug worker in history, occasionally collaborated with regional experts to produce works on geographically restricted faunas. Broadening taxonomic and geographic breadth through collaboration has the potential to increase the stability, universality, and predictive value of classifications. On the other hand, reclusive approaches may produce deleterious results, as for example the near simultaneous but independent work of Knight[60] and Kelton[61] on the genus *Reuteroscopus*. Within Miridae, levels of synonymy are approximately 23%, suggesting that there is room for improvement, with collaboration offering an obvious possibility.

Although many taxonomists have contributed to the plant bug taxonomic literature, just 22 taxonomists have described 75% of plant bug species. Do these 'über-taxonomists' represent the ideal for which we should strive? Obviously, the introduction of species names should not be the only measure by which we judge the output of taxonomists. For instance, the value of Stichel's 316 species names of Miridae is markedly decreased by the subsequent treatment of 285 (90%) of those names as junior synonyms. In contrast, the American entomologist Lattin is not the primary author for any plant bug name; however, just five of his students have produced approximately 750 species group names, with very low rates of synonymy. Nonetheless if we are to attain the rates of taxonomic output necessary to chronicle the diversity of life on Earth, then creating the infrastructure and resources for efficient networks of collaborating taxonomists has the greatest potential for advancing the cause.

13.6 TAXONOMIC, COLLECTIONS AND CLASSIFICATION IMPEDIMENTS

As with many insect taxa, the taxonomic impediment for Miridae exists primarily in the Southern hemisphere, particularly in Australia and Southern Africa. A representation of species richness by country (Figure 13.7) indicates that the plant bug faunas of continental United States, followed by parts of the Palaearctic, Latin America and Sub-Saharan Africa, are apparently the most diverse areas for Miridae in the world. Despite the undoubted high species diversity of plant bugs in these regions, this map is more a representation of sampling bias and the in-country presence of mirid specialists in the twentieth century, rather than a true representation of global species diversity patterns. For example, in Australia the plant bug fauna is represented by about 200 described species, which would signal a depauperate fauna. However, between 1995 and 2001, we have collected at over 400 sites across Australia, resulting in the accumulation of about 100,000 new specimens. These have

FIGURE 13.7 Map of plant bug species richness. The patterns suggest a high degree of sampling bias and correlation with distribution of plant bug taxonomists.

been roughly sorted into 2,000 species, which equates to an order of magnitude increase on published knowledge.

Based on these figures alone, the Australian plant bug fauna would be categorised as one of the most species rich in the world. However, the sampling of the Australian flora is far from adequate. In recent surveys of the Australian Miridae, we have sampled just over 1,200 species of flowering plants and found that 75% of Australian plant bugs are known from only one or two hosts. Although we do not keep records for host plant species sampled without plant bugs, our sampling efforts are to this stage only a fraction of the 18,000 known species of plants comprising the Australian flora. In addition, most localities have only been visited once, and temporal turnover patterns for plant bugs at these localities is largely unknown. In the few cases where there has been repeat sampling, a highly significant temporal turnover in plant bug species has been found[62].

Other factors also contribute greatly to the low rate of species description of insect faunas in the Southern hemisphere, and for plant bugs the lack of adequate generic classifications is a fundamental issue. A historical overview of the description of the Australian Miridae indicates that Northern hemisphere generic concepts were often applied to what we are finding to be a highly endemic Australian plant bug fauna. For instance, *Melanotrichus australianus* Carvalho (Orthotylinae) is the only representative of this genus in the Southern hemisphere. Cursory examination of the species indicates that it is clearly misplaced, and in fact belongs to an undescribed genus in Phylinae. These determinations can often only be made in hindsight; however, it emphasises the importance of quickly building classificatorial frameworks for poorly described faunas.

13.7 PLANT BUGS IN THE TWENTY-FIRST CENTURY: INDUSTRIAL CYBER-TAXONOMY

13.7.1 PLANT BUG PLANETARY BIODIVERSITY INVENTORY

In considering the history and current status of plant bug taxonomy, eroding the taxonomic impediment at an accelerated rate requires an enhancement of collaborative arrangements and applying methods from the information technology revolution. This approach is not unique to the plant bugs and is in line with the strategic rethinking of taxonomy as proposed by others[40,41]. To realise this new taxonomic vision does, however, require significant financial investment, as provided by programmes such as those funded by the US National Science Foundation. One such programme, the Planetary Biodiversity Inventory (PBI), established both a funding programme and articulated goals for undertaking and accelerating taxonomic research. The programme was established in 2003 with the goal of documenting on a global scale the diversity of species rich monophyletic taxa. There were recommendations under the programme guidelines that projects would focus on species description, phylogenetic classifications, global cooperation and information technology.

The Plant Bug Inventory project funded under the PBI programme focuses on plant bug sister subfamilies (Figure 13.5), Orthotylinae and Phylinae. These two subfamilies were chosen as a model group for several reasons. There are significant taxonomic, collection and classification impediments to overcome in this group. Yet there is sufficient existing taxonomic expertise in plant bugs that allows for both generational and international capacity building. Moreover, the documentation of key biological attributes, such as host plant associations, ant mimicry and distribution, allows the outcomes of the plant bug taxonomic research to inform evolutionary and biodiversity research more broadly. In particular, it is envisaged that comprehensive species documentation and the establishment of phylogenetic classifications will allow for studies in coevolution, biodiversity surrogacy and conservation planning, and evolution of ant mimicry. The strategic planning for the first two years of this plant bug project has involved the establishment and development of human, collection and information resources and infrastructure. The key elements that have been implemented and a description of the lessons are as follows.

13.7.2 HUMAN RESOURCES

Large-scale taxonomic efforts can only be accomplished through coordinated effort. Global cooperation guarantees that all participants are working towards unified classification and data standards. In addition, strategic planning allows for a structured division of labour so as to avoid duplication of effort. The Plant Bug Inventory team comprises an international assemblage of established workers, postdoctoral fellows, postgraduate and undergraduate students. These individuals are located in institutions situated in five countries on three continents. As part of this arrangement, dual research hubs were established at the American Museum of Natural History and the Australian Museum, where the development of the information technology, student training and specimen preparation are focused. This degree of centralisation has enabled project management and focused student training. However, it is also crucial that the 'satellite institutions' involved in the project have equivalent access to research tools. This was accomplished through the development of Internet-based research tools as described below.

13.7.3 SPECIMEN RESOURCES AND FIELD WORK

The most important existing specimen sources for information on plant bug diversity reside in approximately 20 institutional collections, mostly in Europe and North America. The collections contain approximately 500,000 specimens of Orthotylinae and Phylinae. Although much information derived from these collections exists in the published literature, that information is not easily recovered digitally from the literature for further use and evaluation. To enable this, the development of a specimen-level database was necessary to incorporate the published information with new survey data.

The need for additional collecting in Miridae, as with most groups of insects, is still great in many parts of the world. Collection priorities were established through the evaluation of existing institutional collections, and coarse-scale mapping of the associated data indicated broad survey gaps. The PBI project collecting has focused particularly on Australia and South Africa, because of the paucity of described species in the face of known high plant diversity[63]. These efforts have produced more than 150,000 specimens in addition to those already available in collections.

13.7.4 PRODUCING DESCRIPTIONS

The Plant Bug PBI team has adopted the approach of producing well documented descriptions, as opposed to totally uniform descriptions across all investigators. This involved the identification of minimal attributes to be recorded, without enslaving investigators to an overly uniform style of description. Because of past knowledge of plant bug systematics, male specimens were used as the primary gender for species delineation. For each species the following attributes have been documented as the minimum data set: illustrated male genitalia; illustrated body form in dorsal view; morphometric measurements in a common format; and scanning and light micrographic images of any additional diagnostic morphological features. This 'minimum set of attributes' can also be tagged and databased to generate succinct web-based 'species pages' that complement the formally published descriptions. In addition to the intrinsic attributes of the species, a minimum set of extrinsic attributes is recorded, which include: host plant species and families; host plant specimen herbarium voucher numbers; collection event data; and point location information and associated hierarchical distributional descriptors.

13.7.5 TECHNICAL RESOURCES

One of our major arguments in addressing the taxonomic impediment both generally and specifically for plant bugs involves the utilisation of web-based information technology. From a research infrastructural point of view, the successful incorporation of an integrated set of information technology tools is regarded as the 'silver bullet' to the global cooperative framework proposed by us, amongst others.
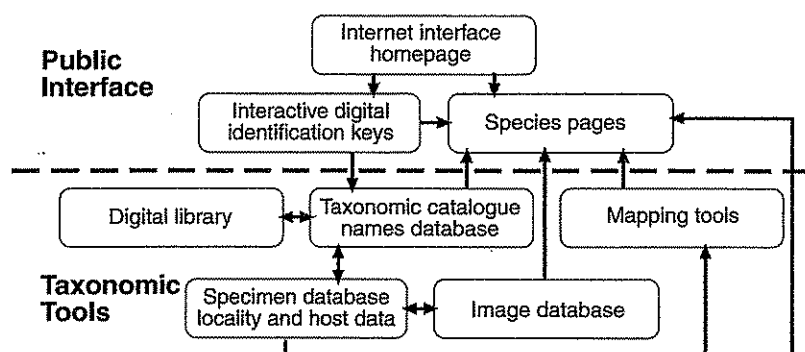
FIGURE 13.8 Information technology infrastructure for the plant bug PBI.

In Figure 13.8 we outline the information technology framework for the Plant Bug PBI project, which is divided into the cyber-based taxonomic tools, and the overarching Internet interface that is designed to provide universal and immediate access to the generated taxonomic outputs. The key cyber-taxonomic tools that are implemented or in development are described below:

Web-based systematic catalogue. Within the confines of available funding and technological understanding, the Plant Bug PBI team has chosen to place as many research tools and as much research information as possible on the Internet. At the core of this approach is a systematic catalogue of Miridae. This source, in the form of a relational database, provides an up-to-date bibliographic history for all taxa in the group under study. It provides a powerful tool for organising and retrieving information on nomenclature, classification, host associations and geographical distributions. The relational database allows for potentially continuous updating and the rapid delivery of identical results to users anywhere in the world, thus maintaining a contemporary species list for Miridae. Beyond its capacity to serve catalogue data, the systematic catalogue serves as a platform for the retrieval of pages from the digital library and other key information from the specimen and image databases.

Digital library. Taking advantage of the relational structure of the systematic catalogue, a digital library of relevant literature, comprising some 30,000 pages has been uploaded to the web in searchable PDF format (http://research.amnh.org/pbi/catalog). These pages relate to the taxonomy, morphology and natural history of Orthotylinae and Phylinae. The most obvious limitation of this approach is that permission for copyrighted material published during the last 70 years could not always be secured, and in such cases this literature is not incorporated into the digital library. Publications that are already available on the web, especially those published very recently, can be included through the use of linking Uniform Resource Locators (URLs). The rewards produced by this digital archive go well beyond its relatively modest production costs. It provides access to a near comprehensive body of primary literature, including access to the older literature, which often has restricted availability, particularly to scientists in developing countries.

Web-based specimen database. Although the structural attributes of specimen data have been widely agreed upon for some time (for example, Darwin Core schema), the approaches to acquiring and retrieving those data are less well settled. In an effort to accommodate the international partners on the Plant Bug PBI team, the project implemented a web-based approach to the acquisition of specimen data. This approach takes advantage of high speed Internet connections and has the desirable property of allowing for centralised geo-referencing, real-time data entry, and the security of using a centralised enterprise level computer server with regular backups and institutional support.

Matrix code unique specimen identification. Whilst unique specimen identification has long been used in vertebrate collections, the 'barcoding' (not to be confused with DNA barcoding) of insect specimens has become a relatively common practice only in the last few years. Unique specimen identification allows for the tracking of information otherwise not possible, and particularly for the

rapid retrieval of database records. Yet the codes may require handling of the specimens in order to be read or might inordinately increase the amount of space required to house collections. The Plant Bug PBI team has adopted the use of 'matrix code' labels, which provide the benefits of unique specimen identification. These labels are relatively small and only increase the total amount of space occupied by the collection by one third. Their small size does not, however, increase specimen handling, as the specimens are machine readable without removing them from the collection.

Real-time mapping/host data from labels. The integration of the specimen database with the systematic catalogue allows for the real-time mapping of species distributions and the assessment of host specificity from actual specimen data. Geo-referenced specimen data can also be easily exported to GIS software for generation of distribution maps for taxonomic manuscripts. Also, voucher material of plants is collected in the field, determined by botanists, digitally scanned and deposited in various herbaria. The host plant data are then linked to specimens through herbaria accession numbers and the unique identifiers associated with plant bug specimens.

High-resolution digital imaging. The description and documentation of taxa can be greatly enhanced through the use of effective imaging and illustration techniques. The Plant Bug PBI team has adopted the use of digital imaging systems that allow for the rapid capture of high-resolution images. These images are supplemented with scanning electron micrographs of specialised morphology. All of these images are databased and linked with specimens, resulting in an image morphological databank for Miridae.

Species pages and integration of information on the web. Using the digitised information sources described above, taxon information is combined into 'species pages' on the web. These displays incorporate real-time nomenclatural, descriptive, host plant, distributional and bibliographic information, as well as morphological imagery. This allows for a comprehensive perspective on the attributes of individual plant bug species. End users may arrive at these pages through Internet search engines, the plant bug online catalogue, or multi-entry web-based identification keys that are being developed by the Plant Bug PBI team.

13.8 CONCLUSIONS

To complete the tree of life we must assemble all of the pieces. The possibility of an endpoint in this task may appear remote, particularly within the lifespan of existing taxonomists. To achieve this goal, the comprehensive documentation of species is a necessary objective, worthy of strategic planning and investment. The insects are a dauntingly diverse taxon, whose complete description and cataloguing in a short time span will take a Herculean effort. In reaching for this outcome, it is important to overcome misconceptions that taxonomy is nothing more than a cataloguing process. Wheeler[41] has made the necessary defence of taxonomy, that it is a hypothesis-driven science. The outputs of taxonomy (such as character homology, taxa and classifications) are the foundation upon which most of biological science rests, and cannot be tossed out for expediency. The speed with which individual investigators can recognise and diagnose new taxa without doubt will occupy some minimum period of time. This is simply part of the analytic process and the fact that species as we understand them are concepts, not self-identifying entities in nature. So the question remains, how do we maintain the cornerstones of traditional taxonomy and ramp up the effort? In this chapter we have argued that the tools of industrial taxonomy must derive from the proper mix of human power, collaboration and technology.

Almost everyone agrees that the World Wide Web and digital technology have the potential to accelerate taxonomy in the twenty-first century. However, the acceleration of taxonomy is not simply increasing the rate of species descriptions, but also greatly enhancing the availability of data to end users. In line with the original PBI objectives, the Plant Bug team has developed and implemented technology that simultaneously assists plant bug taxonomists and enhances broader accessibility of taxonomic data (Figure 13.8). Through the use of relational databases and custom

web applications, users can generate 'material examined' lists for taxonomic manuscripts, track collection data for rare taxa, query morphological and molecular data for phylogenetic analyses, examine image libraries for studies in comparative morphology, or generate the data necessary to build a species richness map for a biological preserve. Furthermore, the integration of these tools with a team-based approach allows for the division of taxonomic effort, while at the same time being able to focus on the larger problem of producing an up-to-date classification for monophyletic groups on a worldwide basis.

Combining traditional taxonomic approaches with global collaboration, centralised web-accessible plant bug data and targeted biological survey work, the Plant Bug PBI has a model for high taxonomic output in Miridae. The success of this project will be judged by those within the taxonomic community, but also by other stakeholders, stretching from the biologically curious to environmental decision makers. Whilst no single investigator can possibly master any megadiverse group, applying suitable web-based technology can effectively couple the skills of multiple investigators working towards a common goal.

ACKNOWLEDGEMENTS

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14 Cichlid Fish Diversity and Speciation

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CONTENTS

ABSTRACT

Cichlids are one of the most species rich families of vertebrates, with conservative estimates citing more than 2,000 extant species. Although native to tropical areas of the world, with the exception of Australia, some 70–80% of cichlids are found in Africa, with the greatest diversity found in the Great Lakes (lakes Victoria, Tanzania and Malawi). Their highly integrated pharyngeal jaw apparatus permits cichlids to transport and process food, thus enabling the oral jaws to develop specialisations for acquiring a variety of food items. This distinct feature has allowed cichlids to achieve great trophic diversity, which in turn has lead to great species diversity. The high species diversity of this vertebrate family is not accompanied by an appropriately high genetic diversity. The combination