

INVITED PAPER

MINIREVIEW

Thysanoptera biodiversity in the Neotropics

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Abstract: It is suggested that descriptive taxonomy of thrips must be integrated into biological studies if we are to understand patterns of evolutionary and ecological diversity. Collecting and describing new taxa is easy, but understanding their position in ecosystems and how they have contributed to the origin and maintenance of biological diversity is more important yet more difficult. Many authors fail to appreciate that individual thrips species are commonly highly polymorphic, both within and between sexes, with the result that 20% of species names and 30% of generic names are currently placed into synonymy. The biological significance of such polymorphism has been little studied, but the presence of large and small males in a species is presumed to indicate some form of male/male competition for resources; this is particularly common in fungus feeding species. Amongst phytophagous species, the recognition of the host plants on which thrips actually breed is a prerequisite to understanding patterns of diversity, some thrips lineages being associated with particular groups of plants whereas others exploit a diverse range of plants. Attempts to understand the diversity of thrips, including the application of cladistic methods, are severely limited by the lack of studies on the biology of individual species, although thrips exhibit a wide range of interesting biological phenomena, including various levels of sociality, gall-induction, specific pollination associations, virus transmission, and ectoparasitism.

Key words: taxonomy, morpho-species, polymorphism, collaborative studies.

Biological diversity can be considered in two different ways. Taxonomists consider the numbers and distributions of taxa, whereas ecologists consider the many ways in which taxa depend on each other – their biological and behavioural relationships. Taxonomy is thus seen as being limited to ‘product’, the publication of descriptions, whereas most research biologists are concerned essentially with ‘process’, how organisms live. If we are to develop an understanding of the functioning and origins of the rich biological diversity of the Neotropics, we need to explore the common ground between product and process. This article is a brief review of the current state of our knowledge of the insect order Thysanoptera, the thrips, considering both taxonomic products and biological processes, with particular emphasis on the Neotropical region.

Thysanoptera are particularly diverse in the Neotropics, with considerably more than 2000 species existing in this Region (Mound and Marullo 1996). These species feed on a variety of substrates, up to 50% being mycophagous either on spores or on hyphae, a large number feeding primarily in flowers, rather fewer feeding only on leaves, even on mosses and ferns, with a few species predatory. In addition to this wide range of feeding habits, the biologies exhibited by these insects include various levels of sociality, remarkable structural polymorphisms within and between sexes, gall-induction on leaves, specific pollination associations, and virus transmission on crop plants. One recent study has even demonstrated ectoparasitism by a thrips species on an Homopteran (Izzo *et al.* 2002). Despite this range of interesting topics, the vast majority of studies on thrips in the Neotropics have been

limited either to insecticide trials or to descriptive taxonomy.

OBJECTIVES OF TAXONOMY

Descriptive taxonomy is essentially subjective, museum taxonomists rarely testing the veracity of the hypotheses they erect, these being the new species that they describe (Gaston and Mound 1993). As a result, many biology students avoid taxonomy, even when recognizing that biological observations need to be viewed in a comparative, evolutionary, framework. This has led to an increasing lack of taxonomic specialists over the last 30 years, and this in turn limits the range of biodiversity questions that can be asked. For example, in tropical forests, neither the ecology of tree flowers, nor the dynamics of leaf-litter systems, can be studied in depth, due to the lack of taxonomic expertise for many of the insect groups involved. Molecular technology is broadening the interest in taxonomy, such tools being seen to provide more objective methods for examining relationships between taxa. But the lack of defined objectives for descriptive taxonomy remains a problem, both for attracting new students and for funding the long-term employment of specialists.

The lack of clarity in taxonomic objectives is curious (Mound 1998). The question "How many species of insects are there?" is deceptively attractive, and has received considerable attention in recent years. Suggestions have been made that funding be sought to describe all of the world's taxa (Anonymous 1994). Even if we assume that a precise answer to this question is possible, the use that could be made of that answer to generate further scientific questions is not clear. Probably as many as 50% of named insect species are based on single samples, even single individuals, with little known either of their biology or their variation. Moreover, probably 5% of named insect species are known only from unrecognizable, although not necessarily old, descrip-

tions. Thus the number of taxon *descriptions* is not a good measure of our knowledge of biological diversity, particularly when, as in some groups, up to 50% of names fall as synonyms, and high synonymy rates remain a modern methodological, not merely an historical, artefact (Gaston and Mound 1993).

In contrast, an apparently similar question, "Why are there so many species of insects?" resonates through most biological disciplines. It involves comparative studies between species and the ways in which they share available resources. It involves species turnover between localities (Bartlett *et al.* 1999), habitats and seasons, and thus requires information on how species disperse, and how they exploit ecosystems that are in a constant state of flux. This one question thus subsumes so many other questions that are fundamental to understanding how biological diversity has arisen, and how we will conserve it. The question "Why?" is about process and opens up new avenues of thought; the question "How many?" is about product and, by itself, is of more political than scientific interest.

THRIPS SPECIES-LEVEL TAXONOMY AND BIOLOGY

Almost 5 500 species of Thysanoptera are currently considered valid worldwide, in nine families and almost 750 genera. Judging from material in the major museum collections there are probably about 10 000 thrips species in the world. The total number of described species from Central and South America is about 1 600 (Mound and Marullo 1996), and more than 700 species of thrips have been described from Brazil. This latter figure suggests that the thrips fauna of Brazil is quite well known, in that a good proportion of the species have been given names. But few of these species can be recognized from the literature, and little is known about how most of them live, beyond that some are probably fungus-feeding, or grass-feeding or flower-feeding.

Problems in descriptive taxonomy

Describing large numbers of species is not simple. For example, more than 150 species are recognized in the genus *Frankliniella* (Nakahara 1997), 120 of these being known from the Neotropics. However, in the collections of the Natural History Museum, London, and the US National Museum, Washington, there are several thousand microscope slides of unidentified *Frankliniella* species from the South American Cordillera. Most of these unidentified *Frankliniella* cannot be sorted satisfactorily even to putative 'morpho-species', because we are unable to distinguish securely between patterns of intra- and inter-population variation. For many, even males and females cannot be associated satisfactorily, due to colour differences between sexes and structural differences between large and small individuals. It is not unusual to find adults of two or more species of *Frankliniella* in the same set of flowers. To establish the intraspecific variation, and the true host plant relationships of a reasonable number of species to provide a satisfactory base-line, requires extensive field-work. Such field studies need to take into account the behaviour of wind dispersed thrips that can be found resting, sometimes in large numbers and in mixed species-assemblages, on plants that are not used for larval development (Mound and Marullo 1996: 17).

A facile response to such real biological problems is to describe as 'new species' each of the structural variants that can be observed, even in the absence of any correlated biological data. One recent example of considerable economic importance concerns the leaf-feeding species of the genus *Scirtothrips*. In Mexico, Johansen and Mojica-Guzman (1999) recorded 21 species of *Scirtothrips* from *Mangifera*, and described 18 of these as 'new species'. However, *Mangifera* is not native to the Americas, hence each of these thrips presumably has a native host plant within Mexico from which it invades cultivated mango trees. The mere description of 'new species' tells us nothing about the functioning of

Mexican biodiversity, particularly the inter-relationships of this important tree crop with the native flora and fauna. In this instance, each 'new species' was defined on trivial structural features that are known to be highly variable within several pest species of *Scirtothrips*. In indicating that such taxonomic conclusions are unreliable, Mound and Strassen (2001) suggested that taxonomic decisions are sometimes too important to other biologists to be left solely to descriptive taxonomists.

Some correlation presumably exists between floristic diversity and the diversity of plant-feeding thrips. But host plant exploitation by thrips ranges from strict monophagy to extensive polyphagy, often within genera. Thus two species of *Echinothrips* are known to be strict monophages, on *Tsuga* and on *Selaginella*, whereas a third member of the genus is a pest on a wide range of plants in greenhouses (Collins 1998). In the genera *Frankliniella* and *Scirtothrips*, a few species are similarly monophagous, although both genera include some of the most extreme polyphagous pest thrips. This unpredictable pattern of host exploitation clearly increases the difficulty of distinguishing intra- from inter-specific variation in museum specimens in the absence of careful field studies.

Problems of species recognition occur in most large genera. Fungus-feeding thrips in the genus *Hoplothrips* show remarkable polymorphism, both within and between sexes. Males and females can look so different from each other that they may be placed in different genera, and extensive population samples are needed to establish ranges of intraspecific variation. Moreover, any attempt to apply one of the 35 species names that are available in the genus from Central and South America requires access to the collections of J.D. Hood at the U.S. National Museum, Washington, because no identification keys have been published. Thus there are serious scientific, as well as technical, problems for anyone in the Neotropics wishing to understand thrips taxonomy and biology.

Research potential

More positively, the problems indicated above can be viewed as offering outstanding opportunities for anyone with serious interests in biosystematics. The polymorphism and structural allometry that is so common in the species of *Hoplothrips*, as well as several other genera of fungus feeding thrips, is known to be associated with competition for resources, including male/male combat (Crespi 1986a, b). Fungus-feeding thrips could provide an excellent tool for investigating various ecological and behavioural phenomena in the Neotropics. Kiester and Strates (1984) described remarkable sub-social behaviour in one large species that lives on the trunks of *Gustavia* trees in Panama feeding on the fungal spores of a lichen species. The adults of this thrips can be observed leading out parties of immatures to particular feeding sites each morning, apparently along pheromone trails, and then leading them back again in the evening to a home crevice in the bark.

Even greater opportunities for innovative biological studies are provided by the species-rich genus *Elaphrothrips*. At times, three or more species of this genus can be found on a single tree, feeding on fungal spores in bunches of dead leaves. But it is not known if two or more species share the same dead leaf, or if they feed on spores of the same fungal species. That is, nothing is known of how such thrips compete for available resources. All *Elaphrothrips* species exhibit variation in male size and body armature, from which it can be concluded that they indulge in male/male competition, but nothing is known for neotropical species of interactions between either con-specific or con-generic individuals occupying the same habitat. The only recent paper on fungus-feeding thrips in the Neotropics (Johansen and Retana 1999), described four new species on a total of seven specimens, all taken in traps. The authors thus provided no supporting biological evidence for their 'new species', and the character states used to differentiate the species are known to be variable within populations of related species

(Mound and Marullo 1996). Such typological taxonomy contributes little to our understanding of biodiversity.

These problems raise once again the question of research objectives. Much taxonomic descriptive work is essentially haphazard, taxa being described as they become available, often for no better reason than that an author wants named specimens in a museum collection. In contrast, description of new taxa is best carried out when this extends knowledge in some specific way, be this of structural variation, host plant relationships, or geographical range; also, it is necessary at times to provide a valid name for a species on which particular observations are being made by other biologists. A contrasting approach to the sequential description of new taxa, as a discipline isolated from the rest of biology, is a research programme in Australia focussed on thrips associated with *Acacia* trees (Crespi and Mound 1997). This programme involves behavioural and host relationship studies, as well as morpho- and molecular-taxonomic studies (Mound and Morris 2001, Morris *et al.* 2002). In Costa Rica, the ALAS (Arthropods of La Selva) Project is another approach that incorporates taxonomy within the broader objectives of field biology. Research programmes with similar broad objectives could be devised on Neotropical thrips, such as the diversity of fungus-feeding species on dead leaves and twigs, or the inhabitants of the flowers of particular plant families in which particular groups of thrips are known to be common, such as Malpighiaceae and Heterothripidae, or montane Asteraceae and the *Frankliniella minuta* group.

A major area for research, still largely ignored, is the relationship between thrips and flowers, whether as pollinators or as pollen predators. In neotropical forests an intriguing problem is the large number of thrips adults that can be found in the fallen flowers of Bignoniaceae trees, these flowers falling daily in large numbers from the canopy to the forest floor. Presumably the adult thrips fly back into the tree canopy to oviposit later in the day, because their larvae are not usually found in

such fallen flowers. However, no life history studies have been attempted on these common thrips, nor is their significance in floral biology understood.

The significance of thrips as pollinators has been largely ignored in the Neotropics, although recent studies have demonstrated that *Frankliniella diversa* is probably a host specific pollinator of *Castilla elastica* (Moraceae) (Sakai 2001), and Del Claro *et al.* (1997) examined the co-existence of ants and a species of *Heterothrips* in the flowers of *Peixotoa tomentosa* (Malpighiaceae). Thrips are not easy insects to work with, but two recent studies on the inter-dependence of a plant species and a host-specific thrips have demonstrated how rewarding such work can be; *Macaranga* flowers in south east Asia (Moog *et al.* 2002), and *Macrozamia* cycads in Australia (Terry 2001). Another interaction between thrips and plants that has been little studied in the Neotropics is gall-induction (Mound and Kranz 1997), although this habit is known in several species of the genus *Holopothrips* (see Mound and Marullo 1996: 290).

THRIPS SYSTEMATICS AND RADIATION

Systematics involves the creation of a hierarchical classification that reflects the presumed phylogeny of a group. One indication of the weak state of thrips systematics is the unusually high number of monobasic genera. Worldwide in the Thripidae, 20 of the 36 genera of Panchaetothripinae, and 100 of the 200 genera of Thripinae, each includes only a single species. Similarly, of the 400 genera of Phlaeothripidae more than 200 each includes only one species. Such a classification is of limited use to other biologists, because it gives no indication of the phylogenetic relationships between species.

The ineffectiveness of a classification comprising so many monotypic genera is particularly important because of the lack of any phylogenetic structure between the sub-family

and genus levels (Mound and Marullo 1996). Relationships between the 250 genera of Phlaeothripinae are particularly difficult to evaluate. The formal suprageneric classifications that have been proposed (Priesner 1960), although commonly quoted, are a poor reflection of relationships. In contrast, the three informal 'lineages' indicated by Stannard (1957), and further developed by Mound and Marullo (1996), are operationally ineffective. Similarly amongst the Thripinae, although many authors quote Tribal names, these Tribes and Sub-tribes are not defined satisfactorily.

Problems in thrips systematics

Intra-specific polymorphism has been mentioned above as an operational problem for species recognition, but such variation also causes problems in establishing generic classifications. For example, species of *Liothrips* usually have a single pair of setae on the head behind the eyes, and males have one pair of setae on the ninth abdominal tergite much shorter and stouter than the other setae. In contrast, several Neotropical species, otherwise similar to *Liothrips* in structure and biology, have been placed in a genus *Pseudophilothrips* because they have two pairs of long setae on the head, and the males have all the setae on the ninth tergite elongate. In studying the biology of one host-specific species that lives on *Didymopanax*, Del Claro and Mound (1996) recognized that both of these character states vary within populations. This is not the only related species in which these character states vary, thus suggesting that *Pseudophilothrips* is, at best, merely a paraphyletic subset of Neotropical species within the worldwide genus *Liothrips*. Again, the absence of data on the host plants of so many of these presumably host-specific species severely limits any consideration of the patterns of variation and radiation in this genus.

The genus *Holopothrips* provides an instructive example of problems in the genus level classification of Neotropical Phlaeothripinae. Mound and Marullo (1996)

recognized 31 species in this genus, but placed five genera as synonyms. However, not all the species exhibit the full suite of character states that define this genus, and the genus is thus defined polythetically (Gauld and Mound 1982). The alternative is to recognize more than 10, mainly monotypic, genera within this lineage and thus obscure any relationships between the species. From the biodiversity viewpoint, the most interesting question posed by this suite of closely related species is their level of host specificity in exploiting the available flora. In the absence of good field studies, this remains unexplored, despite the light that it could shed on phylogenetic relationships within this uniquely Neotropical lineage.

New methods

Molecular tools are giving us new methods of investigating evolutionary relationships, and these techniques sometimes indicate remarkable structural variation within lineages. For example, Bhatti (1992) erected a monotypic family for a remarkable Australian genus *Xaniothrips*. However, not only is this considered an unsatisfactory assessment of the morphological evidence (Mound and Morris 1999), new molecular data (Morris *et al.* 2002) indicate that *Xaniothrips* is closely related to *Koptothrips*, a genus of very different looking species. These two genera comprise kleptoparasitic thrips whose differing methods of invading the domiciles of their host species have led, presumably, to a great divergence in their body structure. Such a lack of congruence between morphological and molecular data poses a problem for traditional descriptive taxonomy, although parsimony applied to the full data set can provide a practical guide.

Parsimony, in the form of cladistics, has been little used in studies on thrips classification, primarily because of operational difficulties associated with homoplasy in structural character states (Gauld and Mound 1982). Cladistics is certainly an important tool with which to handle variation in a rational manner. But cladistic methods must be based on sound

morphology. In one of the few applications of cladistics to thrips in the Neotropics, Retana (1998) prepared a data matrix for 24 character states of 25 species of the genus *Frankliniella*. But in claiming that particular character states were apomorphic for particular groups of species, this author made little allowance for homoplasy. For example, several members of this genus that breed solely on grasses have the head slightly prolonged in front of the eyes. Although this can be interpreted as an apomorphy for an "*F. tenuicornis* group", it is equally likely to be a convergent adaptation to living on grasses, given that it is so common in grass thrips of other genera of Thripidae. Similarly, any attempt to define a genus *Exophthalmothrips* from *Frankliniella* on the basis that some of the facets of the compound eyes are enlarged must specify precisely which ommatidia involved. Clear definition of character states is the basis of sound cladistics, because subtle distinctions in how such states are defined can lead to very different conclusions (Mound *et al.* 2001). Without clear definitions of how character states are evaluated and scored, mathematically sophisticated cladistic analyses (Retana and Soto-Rodríguez 2001) remain of limited use in analysing evolutionary patterns.

FUTURE STUDIES

The Neotropics offer biologists a richly endowed laboratory for investigating evolutionary products and processes. The twin aims of taxonomy – the recognition and naming of species, and the creation of predictive systematic classifications – provide a service to the rest of science by facilitating interdisciplinary communication about organisms. Through its emphasis on evolutionary relationships, taxonomy contributes directly to that ultimate objective of all biological studies – understanding the origins and maintenance of biological diversity. Viewed in this way, taxonomy and systematics have much broader objectives than the mere description and cataloguing of taxa.

However, to achieve such objectives taxonomic studies must involve good field biology in order to recognize structural and biological variation, and where possible must be supported by suitable molecular studies to distinguish species and to recognize relationships. Such an approach requires that taxonomists are viewed, organized and funded as collaborators within multidisciplinary research projects, rather than as isolated individuals working to their own, frequently ill-defined, agendas.

RESUMEN

Se ha sugerido que la taxonomía descriptiva de los tisanopteros (trips) debe integrarse dentro de los estudios biológicos si queremos ser capaces de entender los patrones de diversidad evolutiva y ecológica. Recolectar y describir nuevos datos es fácil, pero entender su posición en los ecosistemas y como ellos contribuyen al origen y mantenimiento de la diversidad biológica es más importante y aún más difícil. Muchos autores han fallado al apreciar que es común que las especies individuales de trips son altamente polimórficas, tanto dentro como entre sexos, con el resultado de que el 20% de los nombres específicos y el 30% de los genéricos son actualmente considerados como sinonimias. El significado biológico de tal polimorfismo ha sido poco estudiado, pero se presume que la presencia de machos grandes y pequeños en una especie indica alguna forma de competencia entre machos por los recursos; lo cual es muy común en las especies que se alimentan de hongos. Dentro de las especies fitófagas, el reconocimiento de la planta hospedera sobre la cual los trips realmente se crían es un requisito para entender los patrones de diversidad, algunos linajes de tisanopteros están asociados con grupos particulares de plantas mientras que otros utilizan un diverso ámbito de plantas. Los intentos de entender la diversidad de los trips, incluyendo la aplicación de métodos cladistas, están limitados severamente por la carencia de estudios sobre la biología de especies individuales, aunque los trips exhiben un amplio ámbito de fenómenos interesantes biológicos, que incluye varios niveles de comportamiento social, inducción de irritación, asociaciones específicas de polinización, transmisión de virus y ectoparasitismo.

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