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Author: Mound, Laurence A.

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HOMOLOGIES AND HOST-PLANT SPECIFICITY: RECURRENT PROBLEMS IN THE STUDY OF THRIPS

Laurence A. Mound
CSIRO Ecosystem Sciences, PO Box 1700, Canberra, ACT 2601, Australia

E-mail: laurence.mound@csiro.au

Abstract

Precise studies on the structure and behavior of thrips can be particularly difficult, due to their small size and restless behavior. As a result, many "host-plant" records are no more than casual "finding places" with limited biological significance. Definitions of "host-plant" are complicated by situations where a plant species provides an important feeding or behavioral resource, but is not used for breeding. Similarly, failure to clearly define some structures on a thrips body, often due to inadequate technical and microscopy skills, can lead to faulty interpretation of species identities and evolutionary relationships. This article re-examines some of these problems.

Key Words: thrips, morphology, behavior, host-plant

Resumen

Estudios precisos sobre la estructura y el comportamiento de los trips puede ser particularmente difícil, debido a su pequeño tamaño y conducta agresiva. Como resultado, muchos registros de "plantas hospederas" no son más que "lugares de encuentro" casuales con un significado biológico limitado. La definición de una «planta hospedera» se complica por situaciones en las que una especie de planta provee un recurso importante de alimentación o de conducto, pero no se utiliza para la cría. Del mismo modo, el hecho de definir claramente algunas estructuras en el cuerpo de los trips, a menudo debido a la insuficiencia de conocimientos técnicos y de destrezas con el microscopío, puede llevar a una interpretación errónea de la identidad de la especie y las relaciones evolutivas. En este artículo se vuelve a examinar algunos de estos problemas.

Palabras Clave: trips, morfología, comportamiento, plantas huésped

In all scientific studies, it would seem self-evident that the attributes to be observed and discussed must be clearly specified and defined. Despite this, in the study of thrips biology and taxonomy it is not unusual to come across published reports that exhibit remarkably little precision in their definition of the reported attributes, whether these are behavioral or structural. This lack of precision is presumably related to difficulties in studying these small insects. Adults can be seen quite readily in the field, but behavioral studies, including association of these adults with their immature stages, and hence discovery of their life history and host-plant dependencies, is difficult and time consuming. Similarly, study of the body structure of a thrips requires great care in the preparation of specimens onto microscope slides to avoid causing distortion or obscuring particular character states. The purpose of this article is to re-examine some of the pitfalls that are apparent in recent publications on thrips, both in the scientific literature and on the web. Nomenclatural details for all thrips names included here are web-available (Mound 2013).

Host Plants of Thrips

Gardeners in the northern hemisphere are familiar with the "Butterfly Bush"—cultivars of the genus *Buddleja* (Lamiales: Scrophulariaceae). Many different butterflies are attracted to, and feed on, the flowers of these garden cultivars, but no northern hemisphere species of butterfly breeds on the leaves of these plants. Because of the lack of breeding, no entomologist would regard *Buddleja* as a butterfly "host plant". Similarly, no entomologist finding an adult moth or beetle on a crop would conclude that the crop was a host for that particular insect species without evidence of breeding. In contrast, it is common for workers on thrips to record as "host" any plant from which an adult thrips is collected. Such records appear to be based on the assumption that if a thrips lands and probes on a plant then it has some association with that plant that at least involves feeding. By applying the same logic, *Homo sapiens* L. (Primates: Hominidae) would be considered a thrips host, because adults of several

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species regularly land and probe the skin on our arms (Bailey 1936; Mound 2004).

Many thrips species are highly dispersive in their behavior and, as a result, adults land on a wide range of substrates, including plants, on which they cannot breed and may not even be able to feed. This landing behavior is exploited in greenhouses through the use of white, blue or yellow sticky traps to detect the presence of pest species, but similar behavior causes problems when large numbers of thrips land on, even insert themselves into, unwanted places, including blocks of white polystyrene used for insulating buildings, and commercial smoke detectors (Lewis 1997; Kirk 2004). From this it is clear that the mere presence of large numbers of adult thrips is not in itself an indication of a host association. This becomes more confusing when an actual plant is involved in thrips landing behaviour. For example, when a *Eucalyptus* tree (Myrtales: Myrtaceae) is in full flower, the gum tree thrips, *Thrips australis* (Bagnall), may be present in vast numbers and many adults will then be found on surrounding plants on which this species is not able to breed. Similarly, Mound & Marullo (1996: 17) referred to thousands of thrips adults being found on the flowering spikes of a species of *Miconia* (Myrtales: Melastomataceae) in Costa Rica, although within two days the flowers and the thrips had gone, and no larvae developed. When a crop is infested by a species of pest thrips, adults of this thrips will drift down-wind, and may then be found on surrounding weeds where they may, or may not, be able to breed. From such observations, it seems that the mere presence of adult thrips on a plant is best considered as fortuitous until proved to the contrary. The only valid conclusion from the presence of adult thrips is that these are dispersive in their behaviour. As a result, many published "host records" for thrips are potentially misleading.

Some published host associations are self-evidently incorrect. The species of the closely related genera *Arorathrips* and *Chirothrips* have larvae with curiously short legs, and these larvae occur only within the florets of Poaceae (Nakahara & Foottit 2012). Despite this, Sanchez-Monge et al. (2011) record *Arorathrips mexicanus* (Crawford) in Mexico as associated with a species of Caryophyllaceae, and Berzosa (1994) records several species of *Chirothrips* in Spain from a wide range of plant families. Records of thrips in these two genera from plants other than Poaceae are based on adults only, and these disperse widely on the wind, including wingless males. Other published host records cannot be refuted so unequivocally, but many that are not supported by numerical and observational data are likely to be unreliable. For example, Sanchez-Monge et al. (2011) record a putatively host-specific species, *Echinothrips selaginellae* Mound, from three common weeds. These authors admit that no larvae were found, but they fail to indicate if their "new host associations" were based on single or multiple adults, or if there was any evidence of feeding.

The identification of larval thrips is a continuing problem in all studies on these insects. It cannot be assumed that larvae and adults found together in a flower necessarily represent the same species. For example, an adult thrips may lay eggs in an Asteraceae flower just as this is opening, but adults of a different thrips species may be found in that same flower when it is fully opened. This resulted in mis-associations of larvae and adults for some common species in the genus *Thrips*, and it was not until careful rearing studies by Speyer & Parr (1941) that the identity of the larvae of several species was correctly established. At present, there is no work on larvae of any thrips genus from the Americas comparable to the precise studies in Europe by Kucharzyk (2010) and Vierbergen et al. (2010).

The production of Pest Risk Analyses by quarantine entomologists sometimes generates spurious results through web searches, but recognising these as such can require careful research. The Australian Quarantine Service requested the present author for information on the status of Kelly's citrus thrips, *Pezothrips kellyanus* Bagnall, as a pest of tree ferns, prior to providing export clearance for such plants. One web-available record had been found to the presence of this thrips on tree ferns in a museum database. However, on checking the collection of that museum it was found that a single female of this thrips had been taken on a tree fern frond during general collecting, and there was no evidence of any real association. More difficult to interpret are records based on multiple specimens, such as the description from Mexico of 18 new species of *Scirtothrips* in the flowers of *Mangifera indica* L. (Sapindales: Anacardiaceae), a plant that is not native to the Americas (Mound & zur Strassen 2001; Hoddle et al. 2008). If these records were found to be valid, with such an extensive array of native *Scirtothrips* species shifting host plants onto mango trees, then export of mango fruits from Mexico might be subjected to quarantine restrictions, with considerable economic implications for the fruit industry of that country. Thus precision in thrips taxonomy and definition of host associations is actually more important to society at large than it is to entomologists.

The World Wide Web has become a potent source for the distribution of dubious information about thrips. Denmark et al. (2006), on a web site issued by The University of Florida Institute of Food and Agricultural Sciences, state that for *Gynaikothrips ficorum* (Marchall), the Cuban laurel thrips, "other common hosts are viburnum, and citrus (Buss 2003)". However, their quotation is clearly wrong because Buss listed viburnum

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and citrus as hosts for greenhouse thrips, but not *G. ficorum*. Denmark et al. (2006) also note that recorded hosts of Cuban laurel thrips from Florida include: "*Codiaeum variegatum, Melicocca bijuga, Nicotiana tabacum, Viburnum suspensum*, and *Citrus* sp. Additional hosts from other areas are *Eucalyptus* in Cuba, *Gliricidia* from Puerto Rico, and *Calocarpum* sp. from Colombia". No precise supporting references are given for any of these host records, although a list of "Selected References" is provided. Ludwig & Drees (2005), on a web site issued by Texas A&M Agrilife, also list the same range of host plants for Cuban laurel thrips, but in the absence of references this is probably due to copying rather than confirmation of the observations. Adults of Cuban laurel thrips fly around actively on warm days, as many Latin Americans will know who, whilst relaxing in the shade of a *Ficus* (Rosales: Moraceae) tree, have picked the thrips out of the glass from which they were drinking. Given that Cuban laurel thrips has been recorded as breeding only on *Ficus microcarpa* L. and its various synonyms (Mound et al. 1996), it seems likely that most of these other host records are based on the presence of adults. Indeed, some seem likely to be based on the adults of other Phlaeothripidae species that are similar in size and general appearance.

One caveat sometimes raised concerning thrips host associations is the suggestion that if a thrips species is a tospovirus vector and probes on a plant, then there is a possibility that a virus might be transmitted. But evidence of tospovirus transmission to a plant species on which a vector thrips is unable to breed has yet to be produced. When considering the biology of a thrips, the plant species that are important to consider, whether in economic entomology or in evolutionary studies, are those on which a thrips is dependent for rearing its young, even if only for one or a few generations. Planning pest control strategies for thrips species, and studying evolutionary patterns in host plant associations, becomes much more difficult if published host records are not based on a recognised definition. Referring to plant species around a crop that "aid and abet thrips species" as "accomplice plant species" (Sanchez-Monge et al., 2011), without defining the function such plants have in the maintenance of populations, lacks the necessary precision. Indeed, weedy plants around a crop may well act as "banker plants" by providing a food resource such as pollen that promotes populations of natural enemies (Wong et al., 2013). For ecological as well as evolutionary studies on insects it is essential to use a precise and meaningful definition of "host plant", and for a thrips species the only practical definition is a plant on which the insect is able to rear its young. Including within the definition those plant species whose flowers provide mating, or even feeding, sites will tend to weaken the value of the definition in the absence of extensive ecological studies.

The converse to the situations considered above of failing to identify a functional relationship between a thrips and plant species, is the not uncommon practice in the pollination, and even ecological, literature of failing to identify an observed thrips species, or even the life stages involved. Thus workers in these fields commonly identify a target organism as a "thrips" or "Thysanoptera". In discussing the pollination of the palm tree, *Chamaedorea pinnatifrons* Jacq.) Oerst. (Arecales: Arecaceae), in Peru, Listabarth (1992) refers to hundreds of small thrips in the male flowers, and further indicates that they breed there, but gives no indication even of the family of thrips involved. Similarly, an experimental ecological study on the effect of mulches on soil fauna in Australia (Nakamura et al. 2009) refers to one of the target organisms assessed as "Thysanoptera" with no indication as to whether adults or larvae were involved, or if the insects were flower-feeding thripids or fungus-feeding phlaeothripids. A curiously similar lack of precision is not uncommon in insecticide trials, with the number of "thrips" recorded pre- and post-treatment (Ullah et al. 2010), but leaving the reader to guess if the figures refer to adults only, or to the more important total feeding population of larvae plus adults. This approach to Thysanoptera is very different from that adopted when the pest under study is a lepidopteran. For many biologists, it seems that thrips are too difficult to examine carefully, and the evaluation of their significance within ecosystems thus remains unsatisfactory.

Thrips Morphology and Systematics

Similar problems in the clarity of definitions can occur among thrips studies within the basic disciplines of taxonomy and identification. "Head length" sounds as though it should be a simple concept but, through lack of definition, references to this length are confusing in much of the thrips literature. Various authors interpret head length differently—from the posterior margin of the head to the anterior margin of the eyes, or to the base of the antennae, or to the apex of the interantennal projection. Another structure that commonly lacks definition is the "fore tarsal tooth", a lateral projection on the fore tarsi of many species of thrips that is useful when describing or identifying species. However, projections on the fore tarsi differ in structure and origin, and to refer to all of them as a "fore tarsal tooth" is misleading. An interesting species of Phlaeothripidae, *Fourbethrips fiorella* Soto-Rodriguez & Retana-Salazar, was described recently from Costa Rica in association with galls induced by a cecidomyid fly (Soto-Rodriguez et al. 2012). This thrips was

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described as having a fore tarsal tooth. However, examination of specimens from the original series has revealed that the tarsal projection is actually a greatly enlarged hamus. This structure occurs in almost all species of Phlaeothripidae, and is a projection from the ventral anterior margin of the fore tarsus. In contrast a "fore tarsal tooth" in Phlaeothripidae is a projection from the inner lateral margin of a fore tarsus. Although possibly sometimes sharing a similar function, these two structures arise in different places on the tarsus and are by no means homologous, and most species with a lateral tooth also have a ventral hamus. Even when small, as in some species of *Karnyothrips*, a fore tarsal tooth always bears the typical set of minute setae that occur on the inner margin of a phlaeothripid fore tarsus, whereas a hamus does not bear setae except at its base. The failure to define and identify the structure of the fore tarsus resulted in the authors of *Fourbethrips* failing to recognise the systematic and biological relationships of their thrips.

Fourbethrips was described as being related to fungus-feeding thrips. This assessment was based on the rather large compound eyes of *F. fiorella* that were claimed to be similar to the holoptic eyes found in three genera of Neotropical fungus-feeding species. However, not only is eye size highly variable among Phlaeothripidae, both between congeneric species and particularly within wing-polymorphic species, but the eyes of *F. fiorella* are no larger than the eyes of *Holopothrips claritibialis* Cavalleri & Kaminski, a leaf-damaging thrips from Brazil. *Fourbethrips* is similar to the species of *Holopothrips* in several characters: the number of sensoria on the third and fourth antennal segments, the presence of an additional pair of wing-retaining setae on the tergites, and a curiously enlarged S-shaped spermatheca in females. No species of *Holopothrips* has any projections on the fore tarsi, but attempting to identify *Fourbethrips* using the key to genera of Neotropical Phlaeothripinae (Mound & Marullo 1996) results in this taxon coming out at *Mixothrips*. This is a genus that is related to *Holopothrips*, but the 2 included species, both of which are gall-thrips on *Eugenia* in Florida, have the fore tarsal hamus greatly enlarged as in *Fourbethrips*. Moreover, several species of *Holopothrips* are known to be associated with galls, and in Guadeloupe *H. inquilinus* was actually described from cecidomyid galls, a host association similar to that of *F. fiorella*. Thus the gall-associated *Fourbethrips* shares a biology and evolutionary origin with the Neotropical leaf-feeding and gall-inducing species of the *Holopothrips* group. It does not represent the striking reversal to phytophagy from fungus-feeding ancestors that would be inferred from the unsatisfactory homology interpretations indicated by the original authors.

Taxonomy provides the data matrix on which all other biologists rely for effective communication about organisms. However, all new taxon names that meet the broad requirements of the Code of Zoological Nomenclature are valid and available, even when poorly founded and with no supporting biology. The published photograph of the holotype female of *Fourbethrips fiorella* shows that this specimen has the fore tarsi partially concealed beneath the mouth cone. Failure to fully clear and spread this specimen will have made critical decisions by the authors about its structure particularly difficult. But many thrips taxa are based on poor quality slide preparations, and this creates extensive, and expensive, problems for all subsequent users of Thysanoptera taxonomy and systematics. For example, description of a single damaged female as a new species, *Neohydatothrips angelorum* Valenzuela-Garcia et al. (2012), will result in long-term recognition problems for which the solutions will be far more costly than the original research (Goldarazena et al., 2008). If taxonomy it is to provide the basic information resource needed by other biologists, then it needs to be based on the best available technical standards, both in field work and in the laboratory.

Conclusion

Just as the incorrect identification of a plant species as a thrips "host" leads to mistakes in our understanding of the biology of thrips species, so the failure to correctly identify the nature of a particular structure on the body, its homology, can lead to a failure to appreciate evolutionary and biological relationships. The detailed biology and structure of thrips can be difficult to study, requiring expertise in field and laboratory techniques, and inaccurate observations have led to a significant proportion of the literature on thrips being unreliable. Mistakes of this sort in the primary literature too often are repeated and thus reinforced in secondary sources, including the world wide web. This can lead to the potential for a cascade of incorrect decisions, whether in pest control planning such as the unnecessary destruction of weedy plants surrounding a crop, or in the more esoteric study of ecological and evolutionary relationships.

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