

# Thysanoptera Phylogeny – the Morphological Background

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The current morphology-based classification of the insect Order Thysanoptera is not based on sound phylogenetic principles. Disagreement exists concerning the level at which the group should be classified. Two sub-orders are generally recognised, and the available evidence suggests a sister-group relationship between these. However, no clear hypothesis of relationships between the family groups, based on defined apomorphies, has been proposed within either of these major groups, and the commonly quoted tribal and sub-tribal classification is clearly artificial. Given that 50% of the recognised genera are monotypic, this paper attempts to set out hypotheses of relationships for future testing by molecular methods.

Keywords: Thrips, phylogenetic relationships, family classification.

Approximately 5500 species are currently listed in the Thysanoptera. The systematic problems within this group can be gauged from the facts that: 1. rather more than 100 family-group names have been proposed (Bhatti, 1990, 1992b); 2. about 50% of the recognised genera are monotypic (Mound, 2002b); 3. many of the supra-generic taxa in common use are not definable by satisfactory apomorphies. The purpose of this paper is to record some of the inadequacies of the current morphology-based classification within the order, primarily to set out some hypotheses of relationships for testing with molecular techniques.

## Ordinal Relationships

The Thysanoptera has been considered to form part of an unresolved trichotomy with the Hemiptera and Psocodea (Psocoptera + Phthiraptera) (Kristensen, 1991). More recently, Yoshizawa and Saigusa (2001) have concluded that, based on the morphology of the forewing basal sclerites, the Thysanoptera and Hemiptera should be considered sister groups, and that together they constitute the sister to the Psocodea. However, the differences between the members of the Hemiptera and Thysanoptera are very considerable. For example, although both have suctorial mouth parts, in bugs these comprise four co-adapted stylets that comprise the paired mandibles and maxillae and these enclose separate food and salivary channels, whereas in thrips only the left mandible develops and this is independent of the co-adapted maxillary stylets that enclose a single channel for both food and saliva. Relationships between these groups remain to be examined further with molecular techniques.

## Thysanoptera – Order, Superorder or Suborder?

The group of insects referred to here as the Thysanoptera has been interpreted in three different ways in recent publications (*Table 1*). Most authors continue to accept the traditional interpretation of the Thysanoptera as a single Order, based largely on synapomorphies provided by the mouth parts and the tarsi. Whilst accepting that these apomorphies can be used to delimit this group, Bhatti (1988, 1992a, 1994) enumerated in excellent detail the many morphological differences between the members of the two suborders, the Terebrantia and Tubulifera. He concluded that the differences are so fundamental that two orders should be recognised, and that the Thysanoptera should be considered as a Superorder with two constituent Orders. This conclusion has not found general acceptance, most students accepting that because the synapomorphies exhibited by the mouthparts and tarsi are good evidence for a single lineage, then the level at which this lineage is classified is of limited importance.

**Table 1**

Thysanoptera: Order, Superorder, Suborder?

Mound et al., 1980	Bhatti, 1988	Zherikhin, 2002
		Order Thripida
		Suborder Lophioneurina
Order Thysanoptera	Superorder Thysanopteroidea	Suborder Thripina
Suborder Terebrantia	Order Terebrantia	Infraorder Thripomorpha
Suborder Tubulifera	Order Tubulifera	Infraorder Phloeothripomorpha

In contrast, Zherikhin (2002) reduced the traditional group Thysanoptera to the level of a suborder, Thripina, that together with a second suborder known only from fossils, the Lophioneurina, comprise the Order Thripida. It should be noted that Zherikhin and his Russian colleagues consider that Ordinal names should be “typified”, that is, that such names should be based on a recognised generic name, although they appear to have put this into practise only for some of the smaller insect orders. However, the presently described members of the Lophioneuridae have very different wings from thrips with more veins and no wing-fringes, they have paired tarsal claws not an eversible tarsal arolium, the number of antennal segments can be as high as eleven instead of a maximum of nine, and Zherikhin suggests that the right mandible was probably well developed rather than vestigial. Curiously, Zherikhin states of thrips (2002: 137) that “in some cases only atrophy of the right mandible is obvious”, although a right mandible is not present as more than a vestige in either larvae or adults of any present day thrips. Association of the fossil Lophioneuridae with the thrips thus seems premature. Moreover, given that the function of names is to facilitate communication, the renaming of the Thysanoptera as Thripina seems impractical, considering that this name is used commonly at Tribal level within the group.

## The Two Suborders of Thysanoptera

Relationships between the two suborders continue to be unresolved by data from morphology alone, with the Tubulifera and Terebrantia either being sister groups (*Fig. 1*), or the Tubulifera being sister to part of the Thripidae within the Terebrantia (Mound et al., 1980). The two suborders provide an interesting contrast, in that the families of the Terebrantia exhibit a more or less progressive series of forms with plesiomorphic to derived character states, whereas none of the members within the single family of the Tubulifera appears to exhibit any character in its plesiomorphic state. This statement might be disputed by Bhatti (1994), and is discussed further below under the section Tubulifera.

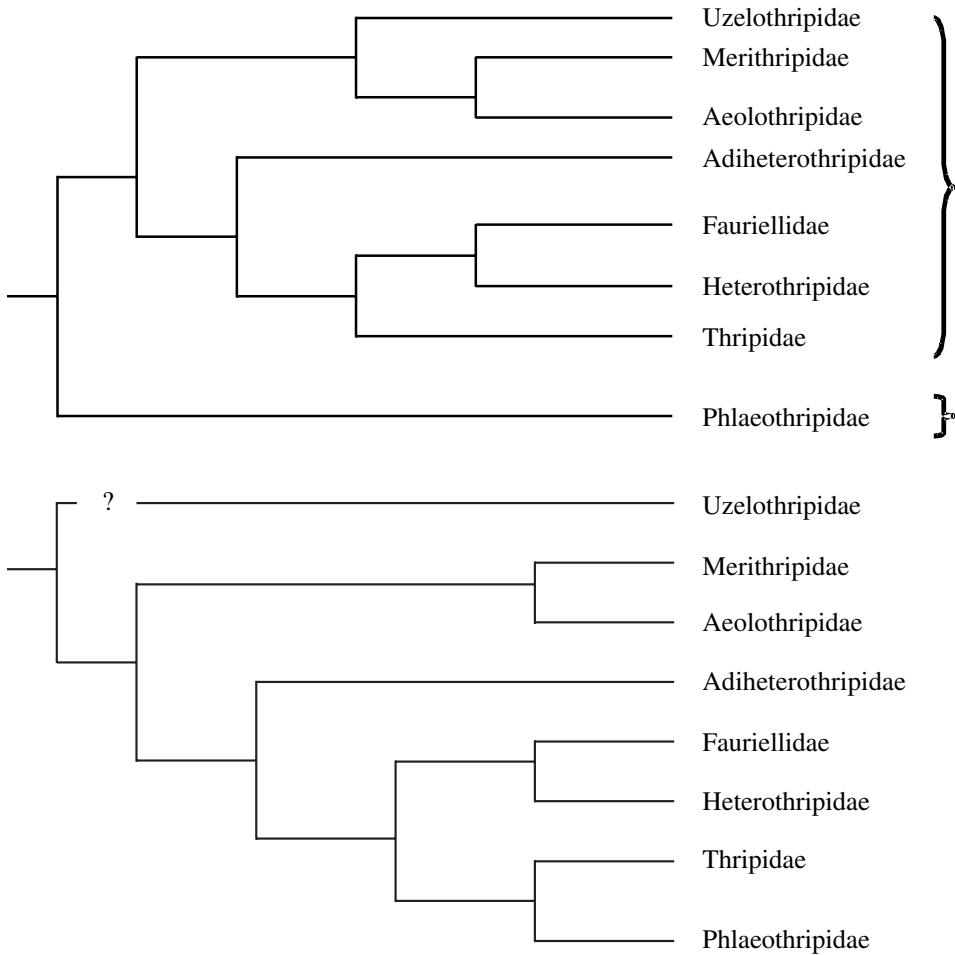


Fig. 1. Thysanoptera family relationships (Mound et al., 1980)

The large number of differences between the members of the two suborders, that have been set out so clearly by Bhatti (1988), lend support to the first of the two evolutionary scenarios. A major problem with this is that, although there are many fossil Thysanoptera that exhibit apparently plesiomorphic character states within the Terebrantia, no fossil proto-Tubulifera have as yet been described. This lack of fossils implies either that the proto-Tubulifera did not live in situations that would result in them becoming fossilised, or that such fossils have yet to be discovered, or that the group evolved relatively late and unusually fast. The second scenario is that the Tubulifera originated through neotenic development from larval Panchaetothripinae within the most highly derived of the Terebrantia families, the Thripidae, and subsequently radiated rapidly. Molecular tools are now needed to examine the relationships between these lineages.

## Family Classification of the Suborder Terebrantia

Currently, the most widely accepted classification of the members of this suborder (Mound, 2002a) recognises eight families, and the names used for these are all derived from extant taxa. In contrast, Bhatti (1989, 1990) recognised the same eight groupings but based some family names on fossil taxa and, moreover, associated the families into four superfamilies (*Table 2*). The family classification system used by both of these authors differs from the traditional classification in distinguishing the Melanthripidae from the Aeolothripidae. European thrips workers continue to place these two groups together, because the members have nine-segmented antennae and the forewings have several cross-veins. However, both these character states are plesiomorphies. No species in the four genera of Melanthripidae shares either of the two synapomorphies of the Aeolothripidae: the loss of paired lobes that represent the eighth sternite, and the elongate antennal sensilla that are linear along the third and fourth segments. One genus of Aeolothripidae, *Rhipidothrips*, is aberrant in having antennal sensilla almost transverse as in Melanthripidae, but these sensilla lack the thickened margins found in members of that family, and the structure is probably due to foreshortening of the linear part of the sensillum, a condition that is known in unrelated Australian species of the aeolothripid genus *Desmothrips*.

**Table 2**

Family classification of Terebrantia

Mound, 2002a	Bhatti, 1989, 1990
Uzelothripidae	Uzelothripoidea; Uzelothripidae
Merothripidae	Merothripoidea; Merothripidae
Melanthripidae	Aeolothripoidea; Melanthripidae
Aeolothripidae	Aeolothripoidea; Aeolothripidae
Adiheterothripidae	Aeolothripoidea; Stenurothripidae
Fauriellidae	Thripoidea; Hemithripidae
Heterothripidae	Thripoidea; Heterothripidae
Thripidae	Thripoidea; Thripidae

Recognition of the Melanthripidae as a family introduces different problems into the classification, because despite their obvious differences in body size and biology, the flower-living Melanthripidae have no well-defined synapomorphies to distinguish them from the fungus-feeding Merothripidae. Most of the species of *Merothrips* are exceptionally small in body size, and hence very reduced structurally, with only eight antennal segments, and the tentorium incomplete. In contrast, the rare species in the two monobasic genera of this family, *Erotidothrips* and *Damerothrips*, are both more robust in build, with nine-segmented antennae and a well-developed tentorium. These species are considered to retain more characters in the plesiomorphic state than any other Thysanoptera (Mound et al., 1980). Marullo and Mound (1995) indicated that not only is *Melanthrips* distinct from the Aeolothripidae, but that within this family the essentially predatory aeolothripids constitute a distinct lineage from the phytophagous aeolothripids (Fig. 2). The relationship between these basal clade families, and to suitable outgroups, is one of the higher priorities in studying thrips phylogeny.

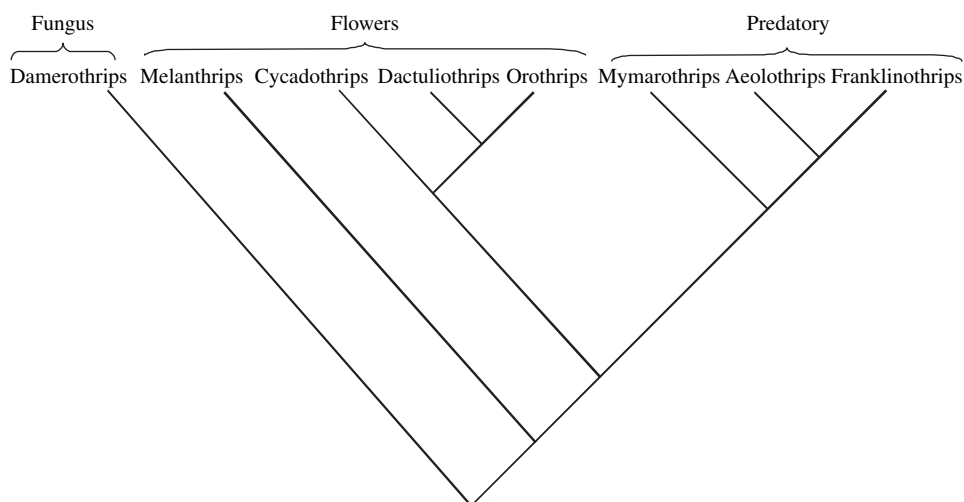


Fig. 2. Relationship between some aeolothripid genera (Marullo and Mound, 1995)

The family Fauriellidae is not a satisfactory grouping, in that it is not characterised by any single apomorphy (Fig. 3). It includes five little known species, in four genera (Mound and Marullo, 1999), and these have a remarkably disjunct distribution between California, south eastern Africa, and the Mediterranean. Moreover, they show a confusing pattern of character states that are intermediate between those found in other families. Despite this, Bhatti (1989) placed the family in synonymy with the Hemithripidae, a family based on fossil taxa each of which is known only from exceptionally poor material. This action was stated to be “based on the published accounts of its type species (especially Mound, 1968: 156, fig. 82)”, although the description and figure quoted contain no information that would allow the living and fossil taxa to be associated unequivocally.

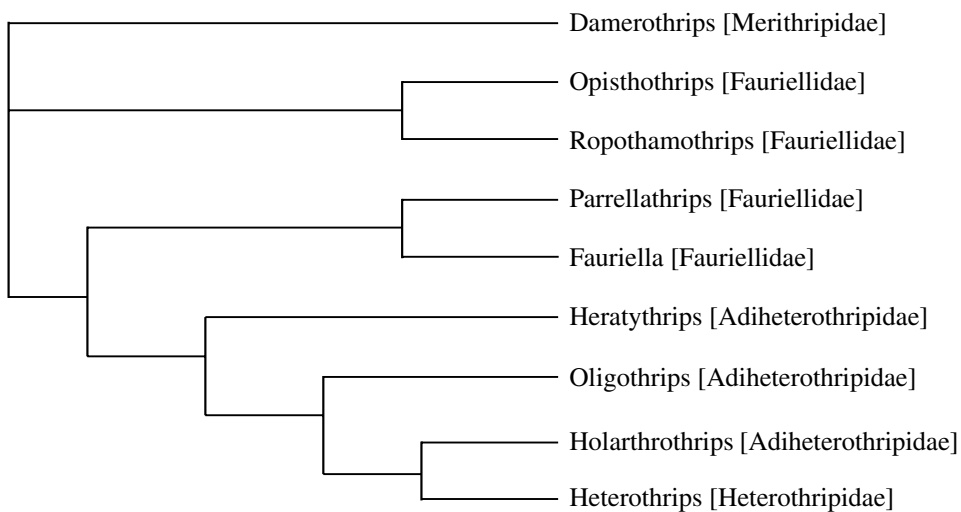


Fig. 3. Generic relationship in Adiheterothripidae and Fauriellidae (Mound and Marullo, 1999)

The family Adiheterothripidae includes three genera and six species, and these also have a disjunct distribution with two species from the west coast of the U.S.A., and four species in the eastern Mediterranean breeding in the male flowers of date palms. These six species share a curious apomorphy in that the antennal sensilla on segments three and four are conical. Sensilla of this form were at one time known only from fossil thrips of the genus *Stenurothrips*, and because of this the group has been referred to by the fossil taxon name, Stenurothripidae (Bhatti, 1989). However, the fossil specimens are too poorly preserved to exhibit anything other than silhouette character states. Moreover, essentially similar conical sensilla have subsequently been described on the fourth antennal segment of *Cycadothrips* species that breed on the male cones of *Macrozamia* cycads in Australia, suggesting that the structure is plesiomorphic. For these reasons, the family name based on living taxa is retained in preference.

The relationships between the genera of the Adiheterothripidae and Fauriellidae were examined by Mound and Marullo (1999) using a data matrix of 20 characters (Fig. 3). The matrix also included data from *Heterothrips* of the family Heterothripidae, as well as of *Damerothrips* of the Merithripidae. The computed relationships (Hennig 86 "ie" with successive weighting) between these taxa failed to find any support for either Fauriellidae or Adiheterothripidae. Thus the relationships between these taxa are another priority for study using molecular data. On present morphological evidence, recognition of a superfamily Aeolothripoidea (Bhatti, 1989) to include the Melanthripidae, Aeolothripidae and Adiheterothripidae is difficult to justify.

The family Heterothripidae comprises four genera and about 70 species, and is found only in the New World. The antennal sensilla of these species are unique within the order, in that they form continuous bands around the apex of the third and fourth segments.

This group of flower-living species presumably evolved after the separation of South America from Africa, but its relationships to the Thripidae and to the two families discussed above remain unclear. Even more equivocal are the relationships of the single species that is placed in the Uzelothripidae. Despite its small size, this species retains the plesiotypic character state of a well-developed tentorium, but the antennae and forewings are unlike those of any other member of the Terebrantia.

## Suprageneric Classification of Thripidae

The seven families discussed above include a total of about 350 species, whereas the Thripidae, the largest terebrantiate family, includes about 2000 species. Currently the 260 genera into which these species are placed are classified into four subfamilies (Bhatti, 1989; Mound, 2002a), Dendrothripinae (10 genera), Panchaethripinae (35 genera), Sericothripinae (10 genera) and Thripinae (210 genera) (Table 3). However, the morphological basis for this classification is weak. Species of Dendrothripinae share only one synapomorphy, an elongate “lyre-shaped” metafurca that presumably provides insertion points for muscles associated with the jumping abilities of the species. However, an essentially similar metafurca is found in the species of several genera of the Panchaethripinae, including *Caliothrips*, *Selenothrips* and *Zaniothrips*. Given that this structure is so evidently associated with jumping, to use it as a means of recognising major groups seems unwise. Similar criticisms can be made of the few character states that are used to define the Panchaethripinae and the Sericothripinae, and the relationships between these groups remain unclear. Currently, these subfamilies seem little more than groupings of convenience. Genera such as *Scirtothrips* have at times been mis-associated with the Sericothripinae, based on the presence of tergal microtrichia, but such surface decoration occurs in many unrelated thrips taxa.

**Table 3**

Thysanoptera families and subfamilies (Mound, 2002a)

Families	Sub-families	Genera valid	Species valid
Uzelothripidae		1	1
Merothripidae		3	15
Melanthripidae		4	65
Aeolothripidae		23	190
Fauriellidae		4	5
Adiheterothripidae		3	6
Heterothripidae		4	70
Thripidae	Panchaethripinae	35	125
	Dendrothripinae	10	90
	Sericothripinae	10	90
	Thripinae	235	1700
Phlaeothripidae	Phlaeothripinae	350	2500
	Idolothripinae	80	700

The large assemblage referred to as the Thripinae ultimately comprises those genera that no taxonomist has been able to separate into distinct sub-groups. In Europe there is a tradition of using Tribes and Subtribes despite these groups never having been seriously defined, and in the context of the world thrips fauna having little or no significance. Thus the Chirothripini is commonly used for a group of grass-living thrips, but there is no evidence that the dominant genera included, *Chirothrips* and *Limothrips*, are closely related (Bhatti, 1989). Similarly, the Aptinothripini is commonly employed for species that lack long setae on the pronotum. But loss of long setae has occurred within several unrelated genera in which the presence of long major setae is otherwise characteristic, including *Thrips* and *Dichromothrips* (Mound, 2002b). The evolutionary relationships and classification of the many genera in the Thripidae thus needs a thorough re-examination, using morphological and molecular data.

## Family Classification of the Suborder Tubulifera

Despite more than 50 family-group names having been proposed for the taxa in this suborder (Bhatti, 1992b), most workers on thrips accept that only a single family should be recognised, the Phlaeothripidae. In contrast, Bhatti (1993, 1994, 1998) recognised 12 additional families (Fig. 4), whilst retaining in the Phlaeothripidae 98% of the described tubuliferan species. Support for these small families is either weak or contentious.

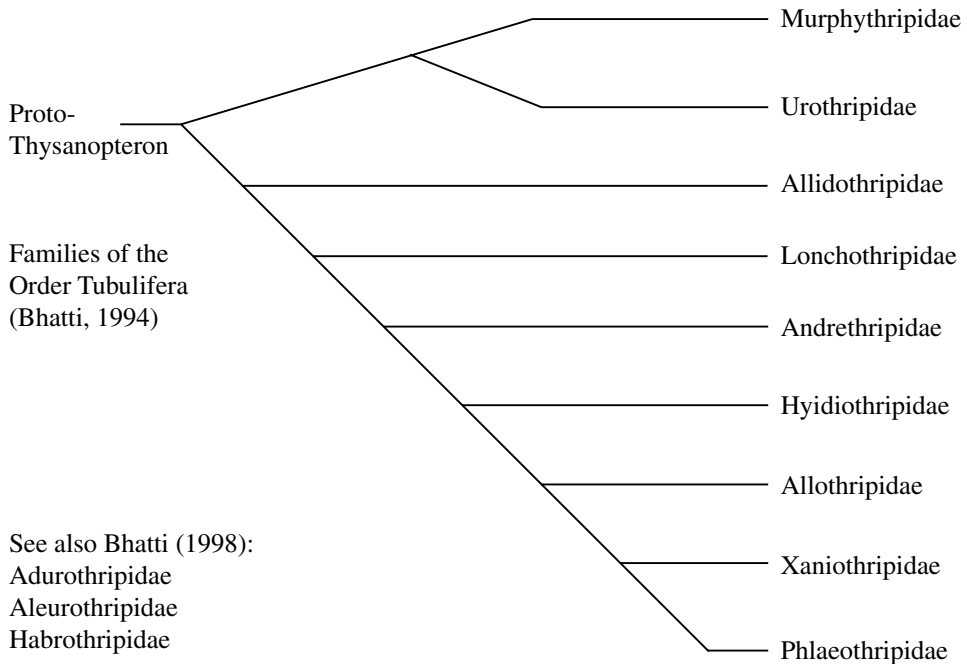


Fig. 4. Some families recognised by Bhatti (1994, 1998)



Xaniothripidae was erected for a single Australian genus that included two species at that time. However, the character states by which the family was defined are not present in both sexes of these two species, and they are also not present in four species that were described subsequently in the genus (Mound and Morris, 1999). Moreover, molecular evidence indicates that *Xaniothrips* represents the sister group to *Koptothrips* within a lineage of Phlaeothripinae that has radiated on *Acacia* in Australia (Morris et al., 2002; Morris and Mound, 2002).

Allothripidae and Lonchothripidae both appear to be based on unusual interpretations of microscope observations. Species in the first are claimed to have a third segment to the maxillary palps, with the proviso that this 'segment' does not bear a sensillum. However, this 'third segment' is actually a greatly enlarged terminal sensillum, and members of the related genus *Parallothrips* have this sensillum only moderately enlarged. The Lonchothripidae was erected for a single species of which it was claimed that the anal setae arise directly from the sclerotised tube (segment 10) not from the anal ring. Examination of a laterally mounted specimen has indicated that the apex of the tube in *Lonchothrips* is greatly asymmetric dorsoventrally (as figured for some *Xaniothrips* by Mound and Morris, 1999), such that the dorsal setae of the anal ring appear to be arising from the surface of the tube when viewed from above. The genus *Lonchothrips* is considered by other authors (Okajima, 1981) as being closely related to *Chirothripoides*, a genus that Bhatti (1998) places in a separate family.

The Andrethripidae was erected for two species that exhibit two remarkable character states; the major setae long and barbed, and the tarsal hamus paired and symmetrical. However, distinguishing a separate family on the presence of these two autapomorphies adds little to our understanding of evolutionary relationships within the Tubulifera. Similarly, the Murphythripidae was erected for one species, and the Allidothripidae for two, all three species being wingless. In *Murphythrips* the prothoracic notopleural sutures are lost, and the first two abdominal tergites are fused to each other. In *Allidothrips* species the prothoracic notopleural sutures diverge anteriorly. However, these character states all occur in unrelated wingless phlaeothripid taxa that live in association with *Acacia* in Australia (Crespi et al., 2004). Apterous thrips commonly have various body parts reduced, and such character states are as likely to be associated with wing loss as to be indicators of phylogenetic relationships.

The Aleurodothripidae was erected by Bhatti (1998) for a single species in which the labro-maxillary complex is amalgamated with the cranium. The author states that this curious fused condition "is a major evolutionary event". However, the significance of this statement is unclear because the author also notes that such fusion has arisen independently at least three times, and he uses this same character state in defining two further apparently unrelated families, the Adurothripidae and Urothripidae.

Of the 12 families distinguished from the Phlaeothripidae by Bhatti (1998), nine include only a single genus (four each with one species, two with two species), and a tenth includes two genera (both with one species). Only the Urothripidae and Hyidothripidae include several genera and a series of species, and both represent lineages whose relationships to the rest of the Phlaeothripidae need exploring with molecular methods. The

Hydiiothripidae comprises about 30 described species in five genera, but Mound and Marullo (1997) suggested that the closest relatives to this group appear to be within the genus *Adraneothrips* in the Phlaeothripidae, and concluded that the hydiiothripines could not be distinguished as more than a genus-group.

The Urothripidae similarly comprises about 30 species, most of which are wingless, in 13 genera, although the group is usually considered a lineage within the Phlaeothripidae (Mound, 1972). In contrast, Bhatti (1994) considered this a family that, together with the Murphythripidae, had separated early from the basal lineage of the Phlaeothripidae (Fig. 4). This conclusion was based on the loss of prothoracic notopleural sutures, and the loss of a suture between the tergites of the first two abdominal segments. However, both of these character states recur in unrelated groups of wingless Phlaeothripidae, and are presumably part of the general reduction in complexity of body form associated with wing loss in Thysanoptera. Loss apomorphies of this type are particularly difficult to evaluate, because they can have multiple genetic origins. Subsequently, Bhatti (1998) removed two monobasic genera from the Urothripidae and erected the Habrothripidae for these, because neither of the species involved have the labro-maxillary complex fused to the cranium.

## Suprageneric Classification of Phlaeothripidae

The removal discussed above, of about 2% of the 3200 species that comprise the Tubulifera to 12 small families, does little to help our understanding of the evolutionary relationships within this suborder, particularly in the absence of clearly defined hypotheses of sister-group relationships. The alternative, traditional, classification of this suborder is, however, equally unsatisfactory. Priesner (1960) recognised a single family in the Tubulifera, the Phlaeothripidae, with three subfamilies, Megathripinae, Phlaeothripinae and Urothripinae. The third of these has been considered above, and is currently regarded as a genus-group within the Phlaeothripinae.

The “Megathripinae”, in practise a junior synonym of the Idolothripinae, is a group of about 80 genera that includes about 600 species, all of which feed by ingesting whole fungal spores (Mound and Palmer, 1983). Two Tribes are recognised, the Pygothripini with six subtribes, and the Idolothripini with three subtribes. Some of this classification appear to have a good phylogenetic basis, with some subtribes restricted in their geographical distributions. However, monophyly of the Idolothripinae itself requires support from molecular data. The members of the group exhibit a great range in life history and body size, from the small-bodied and monomorphic *Allothrips* and *Priesneriella* species that live in leaf litter, to the curious ant-mimicking ground-dwelling *Compsothrips* species, and to the many genera of large-bodied, polymorphic and sub-social species living on dead hanging leaves and twigs, such as *Elaphrothrips* and *Bactrothrips*. Feeding by imbibing whole spores, with the associated broad maxillary stylets and grinding proventriculus, could possibly have evolved more than once. Somewhat similar broad stylets are found in species of one subgroup of the Phlaeothripinae, the Docessissophothripini, although spores have not yet been reported in the gut of any member of this group.

The greatest problem in the classification of the Thysanoptera is with the 2500 described species of Phlaeothripinae. Priesner (1960) erected 10 Tribes within this group, although the vast majority of recognised genera were placed in just three of these (Haplothripini, Phlaeothripini, Hoplothripini). This classification of world genera was in response to a classification of the North American Tubulifera published by Stannard (1957). Both authors evidently struggled to recognise essentially the same three major groups, although Stannard used different names, and Priesner associated many genera differently within the groups. The formal classification proposed by Priesner is clearly not satisfactory, several of the Tribes include a single genus erected for an aberrant species. Mound and Marullo (1996) preferred a modification of Stannard's system in recognising three ill-defined lineages within the Phlaeothripinae. The morphological basis for these lineages remains weak, and they are clearly ineffective operationally, possibly due to the extent of homoplasy amongst thrips (Gauld and Mound, 1982). However, the three groups reflect differences in the life history of the included taxa, and provide a basis for examining relationships using molecular methods.

1. The *Haplothrips*-lineage includes species in which the prosternum retains the anterior pair of sclerites termed basantra, and in which the forewing is usually more or less constricted medially and the fourth antennal segment usually bears four sensilla. These species are mainly phytophagous, commonly in the flowers of Asteraceae and Poaceae, although a few are predatory and some invade galls of other thrips.

2. The *Liothrips*-lineage includes species in which the prosternal basantra are not developed, the forewing is parallel sided, and the fourth antennal segment usually bears three sensilla. These species are mainly leaf-feeding, and many gall-inducing species are involved.

3. The *Phlaeothrips*-lineage includes a wide array of species that feed on fungal hyphae, and because many are highly polymorphic depending on sex and body size, the character states are unstable. However, the forewings are never constricted medially and the prosternal basantra are commonly absent, but the number of sensilla on the fourth antennal segment varies from one to four.

## Summary

The current classification of the insect order Thysanoptera is unsatisfactory phylogenetically. Only relatively recently have thrips taxonomists recognised that many species vary greatly in structure, large and small individuals having at times been allocated to different genera. The behavioural significance of such variation has been examined in few species, although its genetic basis and systematic significance remain unstudied. Given that there is such a limited understanding of the causes and functions of structural variation, within and among species of thrips, it is not surprising that morphotaxonomists have been unable to assess patterns of structural variation within a phylogenetic context. Our next step must be to use molecular and behavioural data to investigate the extent of homoplasy in morphological data, with a view to analysing data sets drawn from different disciplines.

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