The insect Order Thysanoptera: Classification versus Systematics*

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Abstract

Two widely different classifications of the insect order Thysanoptera are discussed; an essentially phylogenetic system recognizing nine families in two suborders, and an essentially phenetic system recognizing 40 families in two orders. This paper emphasizes the distinction between "classification" and "systematics", the former stressing the importance of differences, whereas the latter stresses the importance of derived similarities. A phylogenetic (i.e. systematic) classification incorporates predictions concerning evolutionary relationships that are important throughout biological studies, whether in host and parasite associations, biogeography, comparative physiology or development. The available phenetic classification of Thysanoptera serves no such broader purpose in biology. Recent molecular data derived from the gene 18S rDNA are analysed, but although some groups of taxa are well resolved, the deep relationships within the Thysanoptera remain unclear.

Key words: Thysanoptera, systematics, classification, phylogeny, 18S rDNA

Introduction

Students of the insect Order Thysanoptera sometimes fail to distinguish between the two processes of "classification" and "systematics". A major objective of biological systematics is that classifications should be predictive. That is, in order to be broadly useful across biological disciplines a classification should reflect probable evolutionary relationships. In contrast, it is possible to produce a classification that is merely a record of structural differences. Franz (2005) pointed out a tendency for recent biologists to emphasize systematics at the expense of classification, commenting that "The view that classification matters less and less is neither isolated nor trivially wrong". However, classification sometimes achieves little more than an emphasis, whether detailed or superficial, on the structural differences between organisms; that is, the classification produced informs the reader of no more than is already evident. Even when such structural data are processed through one of the cladistic mathematical packages, differences can tell us little about evolutionary relationships. In contrast, systematics is about recognizing similarities between organisms, and, through shared derived similarities, deducing how and why differences have arisen. Classifying organisms into neatly circumscribed categories has logistic advantages for some levels of communication. However, the real interest in biology lies in deducing how diversification has evolved, and the functional significance to the lives of organisms of behavioural, structural and developmental differences (Heming, 2003).

For the Thysanoptera, the available classification systems are all morphology based. They range from attempts to reflect presumed evolutionary relationships, that is phylogenetic classifications recognising few families, to phenetic systems that emphasise structural differences and recognise many family-level taxa. The objective of this paper is to give an overview of the different systems. We then examine the phylogenetic significance of the available molecular data from thrips, and consider some of the technical problems that appear to be involved in the thrips genome. In this context we present our recent data based on the 18S rDNA gene for 40 thrips taxa, and consider the relationships between these data and morphology-based classifications.

Order, Superorder or Suborder

Traditionally, the nearly 6000 known species of thrips (Mound, 2007a) are placed in a single Order, the Thysanoptera, in which two suborders are recognized, the Terebrantia and Tubulifera (Mound et al., 1980). In contrast, because of the many differences in structure and development between the members of the two suborders, Bhatti (1988) recognised a Superorder Thysanopteroidea, with two Orders. This classification presumably accepted these Orders Terebrantia and Tubulifera as sister-groups within a single lineage, thus the change in taxonomic levels added nothing to our understanding of their relationships. In contrast, Zherikhin (2002) recognised an Order Thripida with two Suborders (Table 1), the Lophioneurina (for some Early Permian to Late Cretaceous fossils) and the Thripina (= Thysanoptera of authors). However, the proposed relationship of the Lophioneurina to the thrips is based on an apparently shared wing form (see Grimaldi et al., 2004; Grimaldi & Engel, 2005), but there is no evidence that the Lophioneurina possessed the remarkable asymmetric mouth parts that constitute the most secure synapomorphy of the Thysanoptera. In the absence of such evidence, this proposed system of relationships remains insecurely founded. Zherikhin also proposed implementing formal "typification" of the nomenclature of this Order, such that the Thysanoptera was renamed Thripina, despite the prior usage of this as a family-group name within the Thripidae. Similar formal typification was not proposed for the other major insect orders treated in the same volume (Rasnitsyn & Quicke, 2002).

**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

TABLE 2. Thysanoptera classification with total genera and species (Mound (2007).

FAMILIES	SUB-FAMILIES	Genera	Species
Phlaeothripidae	Phlaeothripinae	370	2800
	Idolothripinae	80	700
Uzelothripidae		1	1
Merothripidae		3	15
Melanthripidae		4	65
Aeolothripidae		23	190
Fauriellidae		4	5
Adiheterothripidae		3	6
Heterothripidae		4	70
Thripidae	Panchaetothripinae	35	125
	Dendrothripinae	13	95
	Sericothripinae	3	140
	Thripinae	225	1700

Sub-ordinal classification of Thysanoptera

According to the widely accepted, traditional, classification of Thysanoptera (Priesner, 1961), the suborder Tubulifera comprises a single family, the Phlaeothripidae with about 3500 described species, whereas the Suborder Terebrantia comprises about 2400 species in eight families (Mound & Minaei, 2007) (Table 2). The relationship between these suborders remains equivocal. Based on morphological data, Mound et al. (1980) summarized the two obvious possibilities: either the Tubulifera is sister-group to the Terebrantia, or it is sister to a subgroup within the Thripidae (Fig. 1). The morphological and developmental differences are so great, as well summarized by Bhatti (1988, 1992), that intuitively one is driven to consider the suborders as sister-groups. The evidence in support of this, however, is not particularly robust, and Stannard (1957) proposed the second possibility as an alternative relationship. Stannard (1957), and subsequently Mound et al. (1980), indicated that the Tubulifera might have shared a common ancestor with members of the subfamily Panchaeto-thripinae in the Thripidae, presumably diverging from larvae within this group through a process of neoteny. Again, the morphological evidence in support of this suggestion is far from robust, involving presumably convergent similarities. As a result, more recent studies have looked for molecular data to test the two hypotheses of relationships, and this is discussed further below.
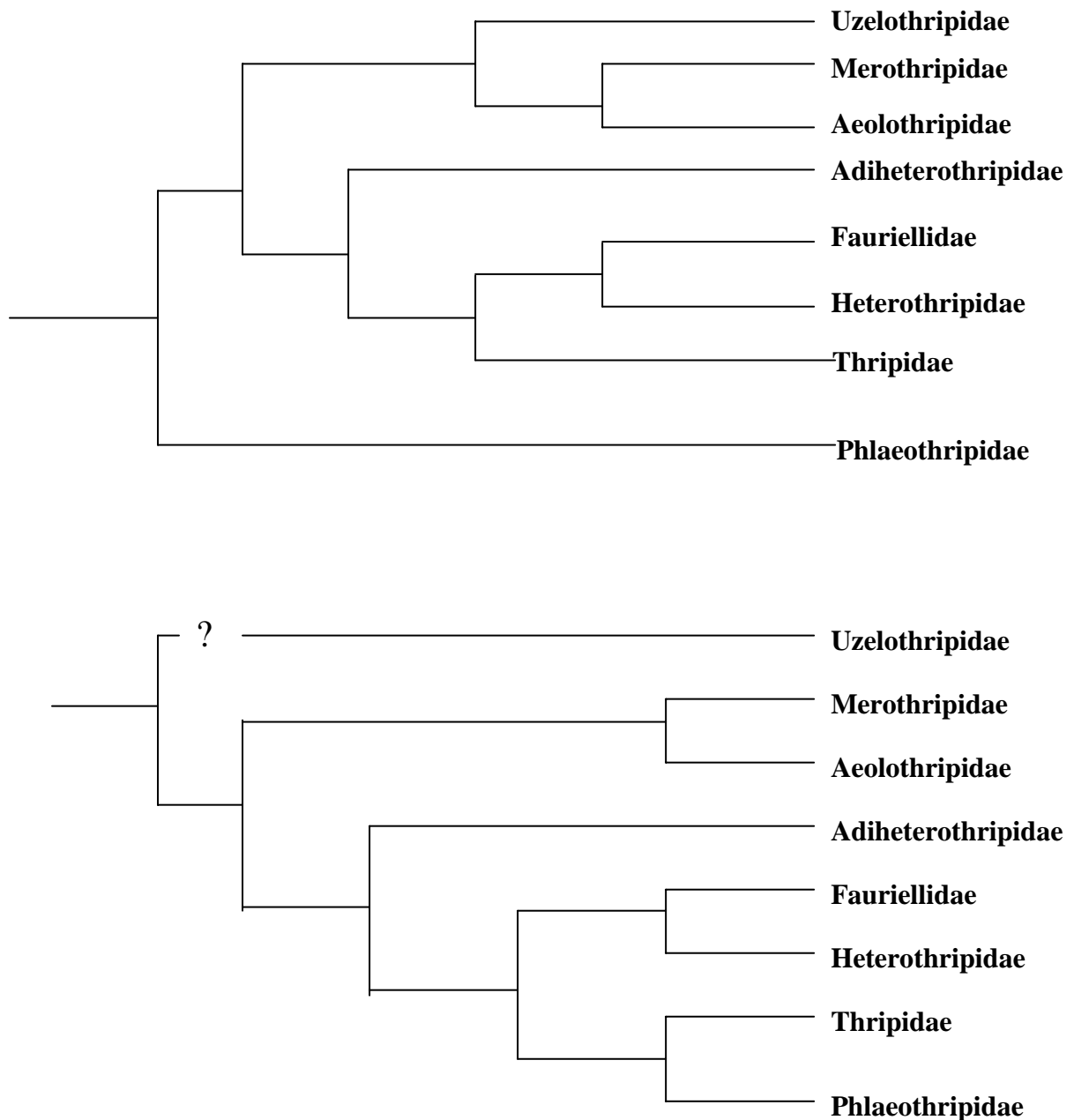
FIGURE 1. Thysanoptera family relationships (Mound, Heming & Palmer, 1980) [This included the Melanthripidae within the Aeolothripidae].

Supra-generic classification of Tubulifera

Monophyly of the Tubulifera is beyond question, and the single family in this suborder, the Phlaeothripidae, is currently considered to comprise two subfamilies. The smaller subfamily, the Idolothripinae, seems likely to prove essentially monophyletic, whereas the Phlaeothripinae is presumably paraphyletic with respect to the larger group. The morpho-systematics of the Idolothripinae, comprising about 700 species in 160 genera, have been examined extensively (Table 3; Mound & Palmer, 1983). In contrast, the relationships amongst the 2800 species and 370 genera of Phlaeothripinae remain unclear, and there have been three very different approaches to the problem.

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TABLE 3. Phlaeothripidae, Idolothripinae: suprageneric groups (Mound & Palmer, 1983).

PYGOTHRIPINI
Pygothripina
Allothripina
Compsothripina
Gastrothripina
Diceratothripina
Macrothripina
IDOLOTHRIPINI
Elaphrothripina
Idolothripina
Hystricothripina

TABLE 4. Phlaeothripidae family-groups recognised by Priesner (1961).

IDOLOTHRIPINAE	**GLYPTOTHRIPINI**
COMPSOTHRIPINI	**LEEUWENIINI**
CRYPTOTHRIPINI	**PLECTROTHRIPINI**
Cryptothripina	**HAPLOTHRIPINI**
Diceratothripina	
Gastrothripina	**RHOPALOTHRIPINI**
Allothripina	**EMPROSTHIOTHRIPINI**
MEGATHRIPINI	**HOPLOTHRIPINI**
Megathripina	Hoplothripina
Idolothripina	Kladothripina
Zeugmatothripina	Dactylothripina
Atractothripina	Williamsiellina
Apelaunothripina	Lissothripina
	Lispothripina
PYGIDIOTHRIPINI	Scopaeothripina
PYGOTHRIPINI	Hoodianina
	Cephalothripina
PHLAEOTHRIPINAE	Mesothripina
	Cercothripina
PHLAEOTHRIPINI	Thorybothripina
Phlaeothripina	Rhinocipitina
Stictothripina	
Aleurodothripina	**TERTHROTHRIPINI**
Thilakothripina	**HYIDIOTHRIPINI**
Macrophthalmothripina	

Phlaeothripinae classification by Priesner

The formal suprageneric classification of the Phlaeothripinae proposed by Priesner (1961) involved 10 tribal and 18 subtribal names (Table 4). This system includes a few useful phylogenetic predictions, but it is essentially phenetic with most of the 28 subgroups based on character states that have little phylogenetic significance. Eleven of these 28 subgroups each contained a single genus, and most of these have subsequently

been demonstrated to have relationships elsewhere, including *Macrophthalmothrips*, *Terthrothrips* and *Emprosthiothrips*. The Kladothripina was an arbitrary assemblage of unrelated genera, and the Hoplothripina was an assemblage of unrelated fungus-feeding and leaf-feeding taxa. The Cercothripinae and the Leeuweni-ini are groups of leaf-galling species (Mound, 2004) that are closely related to *Gynaikothrips*, a genus placed by Priesner in the Hoplothripina. In contrast, the Phlaeothripina is probably a definable lineage of fungus-feeding species, and the Haplothripini is also a recognizable lineage (Mound & Minaei, 2007), although it now includes some of the taxa placed by Priesner in the Mesothripina. Although a brave attempt, this classification fails to take serious account of the morphological and biological attributes of many Phlaeothripine taxa, and does not provide a useful basis for considering the evolutionary radiation amongst these insects.

Murphythripidae
[1 genus; 1 species]

Urothripidae
[13 genera; 30 species]

Allidothripidae
[1 genus; 2 species]

Lonchothripidae
[1 genus; 1 species]

Andrethripidae
[1 genus; 2 species]

Hyidiothripidae
[5 genera; 30 species]

Allothripidae
[1 genus; 30 species]

Xaniothripidae
[1 genus; 6 species]

Phlaeothripidae
[400 genera; 3150 species]

Bhatti (1998) added:

Adurothripidae (1 genus; 1 species)

Aleurodothripidae (1 genus; 1 species)

Habrothripidae (2 genera; 2 species from Urothripidae)

FIGURE 2. Tubulifera familiy relationships proposed by Bhatti (1994).

Phlaeothripinae classification by Bhatti

Bhatti (1994, 1998) is the only other author to have attempted a formal family-level classification of the Tubulifera. This recognised 11 small families, for a total of 96 species, but with over 3000 species remaining in the family Phlaeothripidae (Fig. 2). Eight of the families each contained a single genus, and four of these a single species. Four families were erected for wingless species (although *Allidothrips* and *Allothrips* are both considered to belong in the sub-family Idolothripinae), and some of the character states used, such as a transverse first abdominal tergite (Mound 2007b), are correlated with aptery. This is a typical problem when trying

to assess relationships among Phlaeothripidae taxa; in conjuction with reduced body size, reduction in body structures and wing loss result in "loss-apomorphies" that are of limited value for phylogenetic analyses. Two of the families were erected using character states that can be recognized as misinterpretations: the maxillary palp terminal sensorium in Allothripina is not a third segment (Mound, 2007b), and the apex of the tube in *Lonchothrips* is dorso-ventrally asymmetric so that the anal setae when viewed from above give the erroneous impression of arising on the tube itself. The family Xaniothripidae was erected for one Australian genus that has subsequently been shown to be sister-group to a genus in which the species are structurally very different (Morris et al., 2002; Crespi et al., 2004); there are no grounds for considering *Xaniothrips* the sister-group to the rest of the Phlaeothripidae (Fig. 4). In recognising a family Aleurodothripidae, Bhatti (1998) emphasised that the labro-maxillary complex of the mouth cone is fused to the cranium in *Aleurodothrips fasciapennis*. This fusion was stated to be a "major evolutionary event", yet the same fusion was used by the author to define two other families he recognized, the Adurothripidae and Urothripidae. Thus, all of the family groups recognized by Bhatti within the Tubulifera seem to have little heuristic merit, having been erected by emphasizing the importance of particular structural features with limited consideration of their phylogenetic significance.

Phlaeothripinae classification by Stannard

Stannard (1957) recognized 10 lineages within the Phlaeothripidae, of which one represents the Idolothripinae. The remaining nine Phlaeothripine lineages (Table 5) were subsumed by Mound & Marullo (1996) into three poorly defined groupings that reflect biology and structure to a considerable extent. The smallest of the three, the *Haplothrips*-lineage of flower-living species, has recently been recognized formally as the tribe Haplothripini (Mound & Minaei, 2007). The other two, the *Liothrips*-lineage of leaf-feeding species, and the *Phlaeothrips*-lineage of fungal-hyphae feeding species, provide far greater problems. Adults of species in both of these lineages commonly exhibit remarkable structural polymorphisms, both within and between sexes (Crespi et al., 2004; Mound, 2005), and the large number of "Lines" recognized by Stannard (1957) for the *Phlaeothrips* lineage reflects this structural diversity. Moreover, because much of the published literature on the Phlaeothripinae has developed around the fauna of the northern hemisphere, the systematic problems are greatest when considering the southern fauna. For example, the gall-inducing species (Cavalleri & Kaminski, 2007) in the Neotropical genus *Holopothrips*, as well as many taxa found in Australia (Crespi et al., 2004), do not fit readily into this system. Operationally, the three lineages are clearly not satisfactory in providing a classification, but they are useful in providing a set of hypotheses for testing with further data, including molecular data, and are likely to provide a basis for a formal classification in the future.

TABLE 5. Phlaeothripidae suprageneric Lines and Lineages.

Stannard, 1957	Mound & Marullo, 1996
Idolothrips Line	Idolothripinae
Amphibolothrips Line	*Phlaeothrips* lineage
Docessissophothrips Line	*Phlaeothrips* lineage
Glyptothrips Line	*Phlaeothrips* lineage
Neurothrips Line	*Phlaeothrips* lineage
Hyidiothrips Line	*Phlaeothrips* lineage
Plectrothrips Line	*Phlaeothrips* lineage
Williamsiella Line	*Phlaeothrips* lineage
Haplothrips Line	*Haplothrips* lineage
Gigantothrips Line	*Liothrips* lineage

The supra-generic classification of the Phlaeothripinae thus remains unsatisfactory. Given the extent of homoplasy in the group (Gauld & Mound, 1982), together with developmental processes that give rise to polymorphisms (Crespi, 1988) and extensive sexual dimorphism (Tyagi et al., 2008), it seems unlikely that morphological analysis alone will provide a stable and useful classification that also represents phylogeny.

Supra-generic classification of Terebrantia

The currently accepted classification of the Terebrantia recognizes eight families (Table 2), whereas a re-classification recently proposed by Bhatti (2006) recognizes 28 families and 10 superfamilies for the 2400 species in this suborder (Table 6). This divergence of assessment requires extensive consideration.

TABLE 6. Terebrantia family-groups recognised by Bhatti (2006).

|	
AEOLOTHRIPOIDEA	**RHIPIPHOROTHRIPOIDEA**
Aeolothripidae	Rhipiphorothripidae
Cycadothripidae	
Dactuliothripidae	**STENUROTHRIPOIDEA**
Euceratothripidae	Stenurothripidae
Franklinothripidae	(Adiheterothripidae)
Indothripidae	
Mymarothripidae	**THRIPOIDEA**
Orothripidae	Caliothripidae
DENDROTHRIPOIDEA	Chirothripidae
Dendrothripidae	Heliothripidae
Retithripidae	Panchaetothripidae
HEMITHRIPOIDEA	Parthenothripidae
Hemithripidae	Projectothripidae
(Fauriellidae)	Sericothripidae
HETEROTHRIPOIDEA	Thripidae
Aulacothripidae	Thripinae
Heterothripidae	Dendrothripoidinae
	Tryphactothripidae
MELANTHRIPOIDEA	
Melanthripidae	**UZELOTHRIPOIDEA**
	Uzelothripidae
MEROTHRIPOIDEA	
Erotidothripidae	
Merothripidae	

Lower families of Terebrantia
Among Thysanoptera, the Terebrantia includes all of the species that are considered to have retained the largest number of characters in the plesiomorphic state. Thus members of the first four families listed in Table 2 all have a well-developed tentorium, whereas this structure is scarcely apparent in the head of members of the remaining four families listed. Uzelothripidae is known only from one species, and in this the structure of the antennae, abdomen and forewing is difficult to relate to that of any other thysanopteran (Mound et al., 1980). In the families Merothripidae and Melanthripidae, females retain two distinctive characters in the plesiomorphic state: abdominal sternite VIII is retained on the posterior margin of sternite VII as a pair of lobes bearing two pairs of setae (absent in all other Terebrantia); abdominal tergite X retains a pair of trichobothria on the posterior margin (greatly reduced in some species of Aeolothripidae, but otherwise absent in the other Terebrantia). In the northern hemisphere, Melanthripidae are distinctive in being large and conspicuously setose, whereas in Australia several species are small and pale with short setae. These species are no larger than *Erotidothrips mirabilis* in the Merothripidae, and the structural character states that have been used to distin-

guish these two families are less easily defined. Bhatti (2006) distinguishes these families on the basis that the forewings of Melanthripidae are broad, but those of Merothripidae are more slender, and he cuts the phylogenetic Gordian knot by placing *Erotidothrips* in a separate family. The biological differences are clear, members of Melanthripidae breed in flowers, whereas members of *Merothrips* and *Erotidothrips* are fungivorous. However, there seems to be no synapomorphy linking the two families, despite the shared plesiomorphies (including structure of the antennae).

*Relationships within Aeolothripidae*

The family Aeolothripidae is distinguished from the previous three families because, despite retaining the tentorium in the plesiomorphic condition the eighth sternite is not developed at all (although the two pairs of setae associated with that sternite are retained as submarginal setae on the seventh sternite). Bhatti (2006), in recognizing this family as a superfamily, distinguished a further seven families, each for a single genus (Table 5). The family Euceratothripidae was distinguished because the single known specimen, a male from Peru, has exceptionally elongate and convoluted sensoria on the antennal segments. But other species within the Aeolothripidae are also known to have elongate, wavy, sensoria, such as the Australian species *Desmothrips steeleae*. There is thus no reason to consider *Euceratothrips* as sister-group to any substantial part of the Aeolothripidae, as is implied by placing it into a separate family. *Indothrips* shares sufficient character states with *Mymarothrips* for these to be considered sister-genera (Tyagi, et al., 2008), and moreover, these two seem likely to be the sister-group to *Franklinothrips*; placing each of these three genera into their own families only obscures such relationships. The remaining three monobasic families distinguished by Bhatti (2006) are interesting because, unlike most Aeolothripidae, the species involved appear to be phytophagous rather than predatory (Fig. 3), but it remains far from clear whether they comprise one or more clades (Marullo & Mound, 1995).
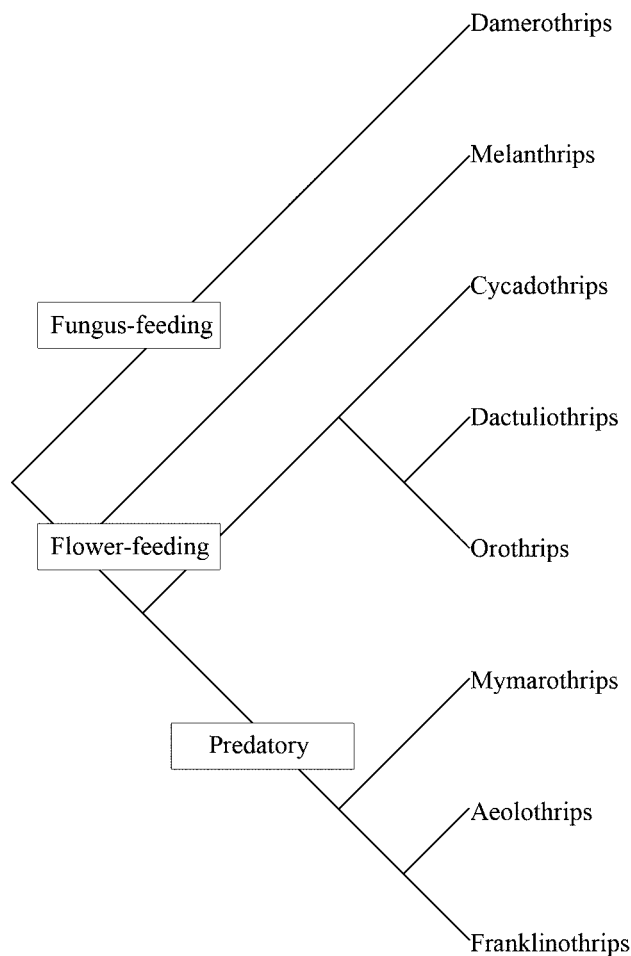
FIGURE 3. Relationships between some genera of Aeolothripidae (Marullo & Mound, 1995).

Intermediate families of Terebrantia

The vast majority of Terebrantia species are placed in the Thripidae, but relationships between the other three families indicated in Table 2 are not clear. Bhatti (2006) places each of these families into its own super-family, and also uses a different nomenclature for two of these. The family Fauriellidae is referred to as the Hemithripidae, but the latter name derives from a heavily distorted Baltic Amber fossil on which no critical structural details are visible (Mound, 1968). The Fauriellidae exhibits a discontinuous distribution, with species in California, southern Europe and South Africa, but there is little evidence to indicate that the five species involved (Fig. 4) constitute a single clade (Mound & Marullo, 1999). Adiheterothripidae is referred to by Bhatti (2006) as the Stenurothripidae, but this name is also based on fossil specimens on which structural details cannot be observed. Species of Adiheterothripidae occur in California and in the Mediterranean region through to India, and although they have characteristic antennal sensoria there is, again, limited evidence that the three small genera involved (Fig. 4) constitute a single clade (Mound & Marullo, 1999).
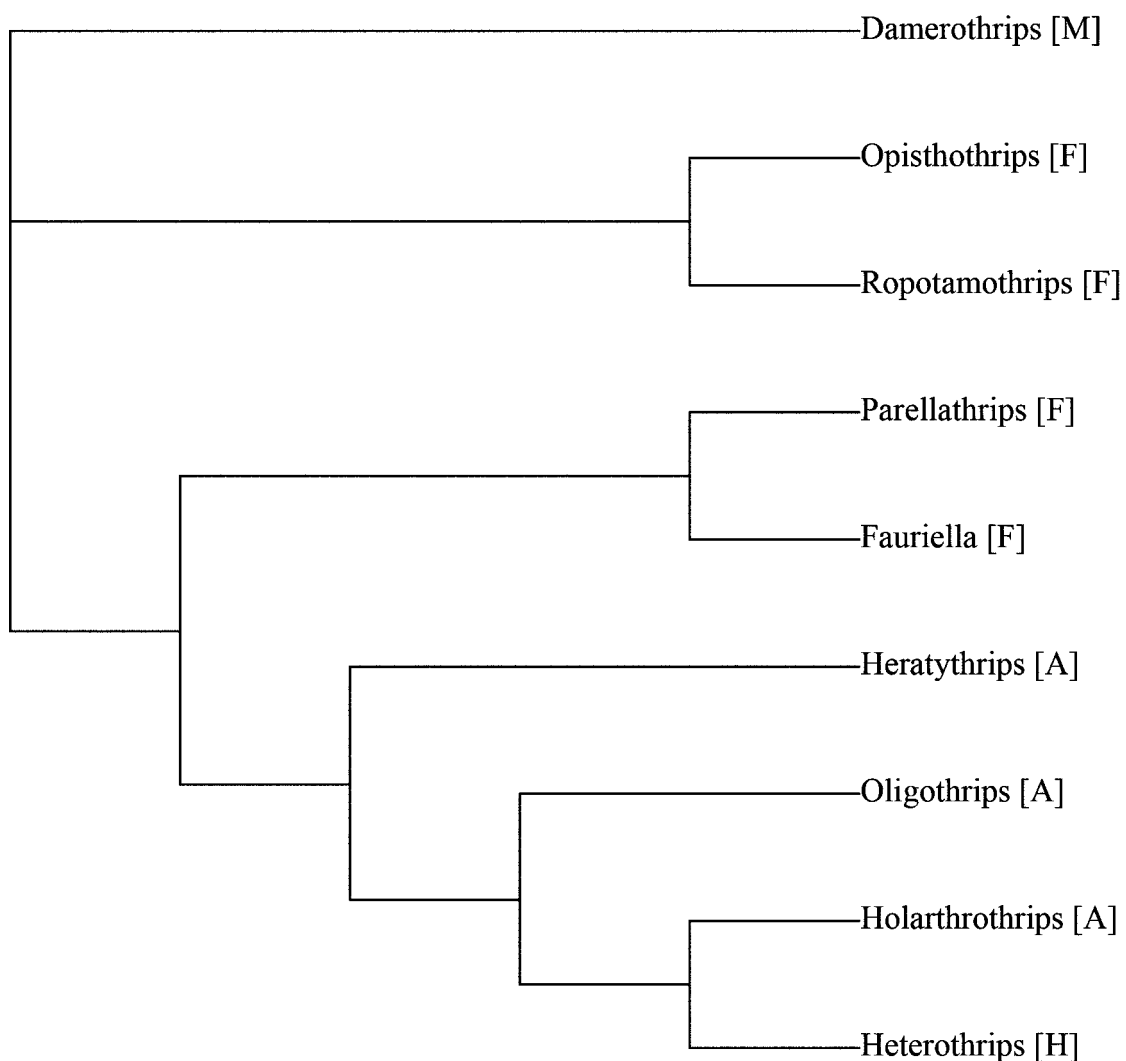
FIGURE 4. Relationships between the smaller families of Terebrantia (Marullo & Mound, 2001).

Heterothripidae species are found only in the Americas, and the family Aulacothripidae was distinguished by Bhatti (2006) from these because the only known species has convoluted antennal sensoria (Table 6). However, *Lenkothrips* species in the Heterothripidae also have sensoria greatly elongate and curved (Mound et al., 1980: Fig. 23). *Aulacothrips dictyotus* is certainly a remarkable insect, the only known ectoparasitic thrips

(Izzo et al., 2002), and the abdominal structure with protective devices for the wings presumably reflect this habit. There is no evidence to support a sister-group relationship between this species and the rest of the Heterothripidae, such as would require a separate family.

Relationships within Thripidae

Within the Thripidae four subfamilies are currently accepted (Table 2). However, the morphological support for these groups is not strong, and relationships between the 360 species placed in the three smaller groups and the 1700 species in the Thripinae are not clear. The 35 genera in the subfamily Panchaetothripinae appear to form a monophyletic group, although Bhatti (2006) separated these genera into five families. The transfer of 25 genera to the Heliothripidae was accompanied by the statement that the included species "cannot be placed in the same family as *Panchaetothrips*", which genus of six species was placed in its own family. This statement receives partial support from an earlier phylogenetic analysis of the group (Mound et al., 2001) that placed *Panchaetothrips* and *Heliothrips* within separate sub-clades, together with some other genera of the Panchaetothripinae. A family Tryphactothripidae was distinguished by Bhatti because the sculpture on the head is raised. However, the extent to which reticulation is raised into a honeycomb-like structure varies across the head of single individuals. The variation between species in reticular elevation is merely an exaggerated growth process, resulting from increased deposition of cuticle at the margin of epidermal cells. Species placed in the Tryphactothripidae share a remarkable autapomorphy with some taxa placed into the Heliothripidae: tergite two bears laterally many sharply recurved microtrichia. A family Caliothripidae was distinguished for a single genus in which species share the autapomorphy of a coiled apodeme or tendon in the hind coxae, and Retithripidae was recognised for a single genus of two species that have unusual forewings with blister-like swellings, and an enlarged metasternellum.

Bhatti discussed the possibility that some of the structures recognized in his re-classification might be associated with the habit of jumping, but then dismissed this as a matter of conjecture. However, given that many Terebrantia have the habit of jumping before flight take-off (Ellington, 1980), it is not surprising that a variety of adaptations to facilitate such behaviour have evolved. In particular, Bhatti's newly erected families Caliothripidae, Retithripidae and Dendrothripidae (Table 5), were distinguished because of particular thoracic structures, but field experience with species in each of these groups suggests that the normal Thripidae take-off jump has been perfected into an escape mechanism. Certainly members of these groups have remarkable jumping ability, particularly in warm sunshine. The various structural divergences seem more likely to have arisen independently within the currently recognized lineages, and cannot be taken as evidence for sister-group relationships to other parts of those lineages.

Both of the other two small subfamilies of Thripidae that are generally accepted were recognized by Bhatti (2006) at family level. The subfamily Dendrothripinae is a group of about 95 leaf-feeding species, in 13 genera (Mound, 1999), that share structural character states with some species in the Panchaetothripinae. Finally, the subfamily Sericothripinae is a single lineage of three weakly-distinguished genera (Wang, 2007), with about 140 species that have a characteristic forewing chaetotaxy, but whose relationship to the rest of the Thripinae is unclear. Historically, the species in the Sericothripinae resemble those in the genus *Scirtothrips* in having numerous rows of microtrichia on the abdomen, but this is no longer considered to indicate a close relationship (Masumoto & Okajima, 2007).

Various family-group names have been proposed for particular groups of species within the Thripinae. Thus species that lack elongate setae on the pronotum have been segregated to the Aptinothripina, but this is clearly a polyphyletic group based on a classic "loss-apomorphy" that recurs in several distantly related Thripidae. Similarly polyphyletic is the Humboldthripini, erected for unrelated species with pronounced sculpture on the pronotum (Johansen & Mojica-Guzman, 1996), and Pseudothripini (Retana Salazar, 2000) erected for a group of unrelated Neotropical species that share the equally uninformative character state of nine antennal segments. Bhatti (2006) recognized a new family, Chirothripidae, for a group of closely related

genera in which all of the species breed within the flowers of Poaceae (Table 6). However, the unusual structure of the head and thorax of species in *Chirothrips* and related genera is presumably related to their curious biology that involves each larva pupating within an individual "seed" of a grass species. Bhatti similarly erected the family Projectothripidae (Table 6) for a single genus in which the species live on *Pandanus* flowers and have a uniquely elongate eighth antennal segment, also the subfamily Dendrothripoidinae for a single genus in which the species have remarkably robust microtrichia on the abdomen. Such emphasis on particularly unusual autapomorphies provides no indication of relationships.

The extensive family-group re-classification within the Terebrantia proposed by Bhatti (2006) was accompanied by a great deal of excellent morphological detail, but it involved little discussion of relationships. That proposed system is here considered to be essentially phenetic, showing limited phylogenetic basis. Indeed that author states that "Interpretation of their phylogenetic relationships is beyond the scope of the present study since that would require, at first, generation of massive data to bring out the numerous structural peculiarities of many taxa of these insects." These peculiarities are here considered to be exceptional autapomorphies, that thus cannot provide us with more than limited information on relationships. Because of this, it seems unlikely that the proposed families can find general acceptance.

Considerations from molecular data

The first attempt to use molecular data to investigate relationships within the Thysanoptera (Crespi et al., 1996) used the 18S rDNA gene from three species of Terebrantia and three of Tubulifera. Not surprisingly, this recovered the appropriate two groups as two distinct clades. Using the CO1 gene for eight of these species produced further, but weak, support for these two clades. Not surprisingly, there was little that could be reliably deduced from such a limited taxon selection. Subsequently, a data set was produced of approximately 600bp of 18S rDNA from 52 Thysanoptera species (18 Tubulifera, 34 Terebrantia), representing seven of the nine families (Morris & Mound, 2003). These sequences were aligned with sequences from nine outgroup taxa (Hemiptera, Phthiraptera and Psocoptera species from Genbank). Analysis of these data produced a result that was a good first approximation of thysanopteran phylogeny, but was not sufficiently robust to test adequately hypotheses of relationships within the order. This was largely due to the paucity of informative characters contained in a single, relatively short DNA region. One solution explored here was to increase the length of the sequences studied. Other gene regions have been examined for phylogenetic utility in this group but as yet few good candidates have been found. Crespi and coauthors (1996) found that COI provided some support but was highly divergent and thus could be saturated to a large degree. Other potential genes such as EF1a have been used for phylogenetic studies within Thysanoptera but, as in many insect orders, the gene exists as at least two paralogous copies in thrips and thus presents difficulties in determining homology with increasing divergence between taxa. As with many insect groups, thrips have often not amplified readily for 'universal primers' and this is perhaps part of the reason for the lack of good progress towards an ordinal-level molecular phylogeny for this group.

Ribosomal DNA is often used in studies of higher-level systematics in arthropods for several reasons, and yet the analysis of these regions is not entirely straightforward. Gene regions such as 18S and 28S are used frequently because they exhibit levels of variation appropriate to higher-level systematics questions, and because they are present in multiple copies in the genome and tend to amplify readily using standard primers. The disadvantages lie in the problems of alignment of the data, and the effects that alignment can have on subsequent analysis. Because rDNA consists of a range of highly conserved to highly variable regions due to its secondary structure, the alignment needs to be repeatable and testable.

In the present study, the data set of 18S sequences was expanded to incorporate approximately 1800bp of 18S rDNA and to these were added three thysanopteran sequences taken from Genbank, giving a total of 38

species of Thysanoptera, representing eight of the nine families. The family not included, the Fauriellidae, is known from only five species and, to date, has not yet been sequenced. The 18S data were supplemented with 12 paraneopteran sequences taken from Genbank and were aligned manually using the secondary structure model as proposed by Kjer (2004). Regions of uncertain alignment were excluded using the criteria of Kjer (1997) and maximum parsimony (MP) and maximum likelihood (ML) analyses were conducted using PAUP*4.0 (Swofford 2002).

Likelihood and Parsimony analyses of these data produced results that in many ways reflect the conflicting hypotheses of relationships arising from morphotaxonomy. This is a result of the difficulties of trying to establish relationships between fundamentally different groups. The parsimony analysis (Figure 5) produces a phylogram much like the result given by earlier analyses of a short fragment of 18S (see Morris & Mound, 2003), with Phlaeothripidae and Panchaetothripinae appearing to be distinct basal lineages. However, the likelihood analysis (see Figure 6) collapses most of the resolution at the base of the thysanopteran clade and places these two lineages well within the main thysanopteran clade. This significant difference between these two results is not as disastrous as it may seem, in that it serves to highlight those areas within the phylogeny that are fundamentally unstable and highly dependent on alignment parameters and analysis methods. The weakness of parsimony methods in resolving long-branch relationships has been well documented, and it is likely that this is the cause of a large part of the differences seen in these results. However, the results also exhibit a number of very short internal branches with little support and this suggests that, while some groups of Thysanoptera are distinct, there is little in our data to inform us about relationships at the base of the thysanopteran lineage.

The most reassuring aspect of the resulting phylograms is that the monophyly of the Thysanoptera remains robust in both analyses. However, the two major clades within the Thysanoptera continue to be surprising, with the Terebrantia rendered paraphyletic with the Tubulifera nested within. The Tubulifera is recovered as a monophyletic group but its relationship to the rest of Terebrantia remains uncertain. The sub-family Idolothripinae is monophyletic within a paraphyletic Phlaeothripinae as is expected based on morphology. The taxa represented in this analysis provide little information as to possible structure within sub-family Phlaeothripinae, except to say that the proposed family Xaniothripidae (Bhatti, 1992) seems to be unsupported given the close relationship seen between *Xaniothrips* and other Phlaothripinae with more 'typical' morphology (e.g. *Gynaikothrips*).

The Thripidae subfamily Panchaetothripinae is perhaps the least stable group, flipping from a position at the base of Thysanoptera in MP analyses, to a position well within with the Terebrantia clade in ML analyses. The clade containing Panchaetothripinae seems to be particularly strongly supported, contrary to the morphology-based conclusions of Bhatti (2006) discussed above. However, significantly more data are required before any firm conclusions can be drawn on the relationships of this sub-family to the remainder of Thysanoptera.

Within the main Terebrantia clade, three disparate genera of Aeolothripidae form a robust single clade in both analyses, emphasising the distinctiveness of this family, although the aberrant Australian genus, *Cycadothrips*, remains outside this clade. The morphology-based distinction of the Melanthripidae from the Aeolothripidae is well supported, with the three represented genera (*Cranothrips*, *Ankothrips* and *Melanthrips*) comprising a separate clade. The association of *Heterothrips* with *Holarthrothrips* (Adiheterothripidae) and *Oligothrips* is not surprising, but neither *Merothrips* nor *Uzelothrips* associate with any other taxa.

Within the Thripidae clade it is interesting to note that *Frankliniella* and *Thrips* are associated, although the *Thrips* species are on curiously long branches. In contrast, some genera appear to be in locations not predicted by current understanding of their morphology, such as *Pseudanaphothrips* and *Pezothrips kellyanus*. This is possibly an artefact of the analysis, or even could be due to mislabelling or contamination of the sequences.
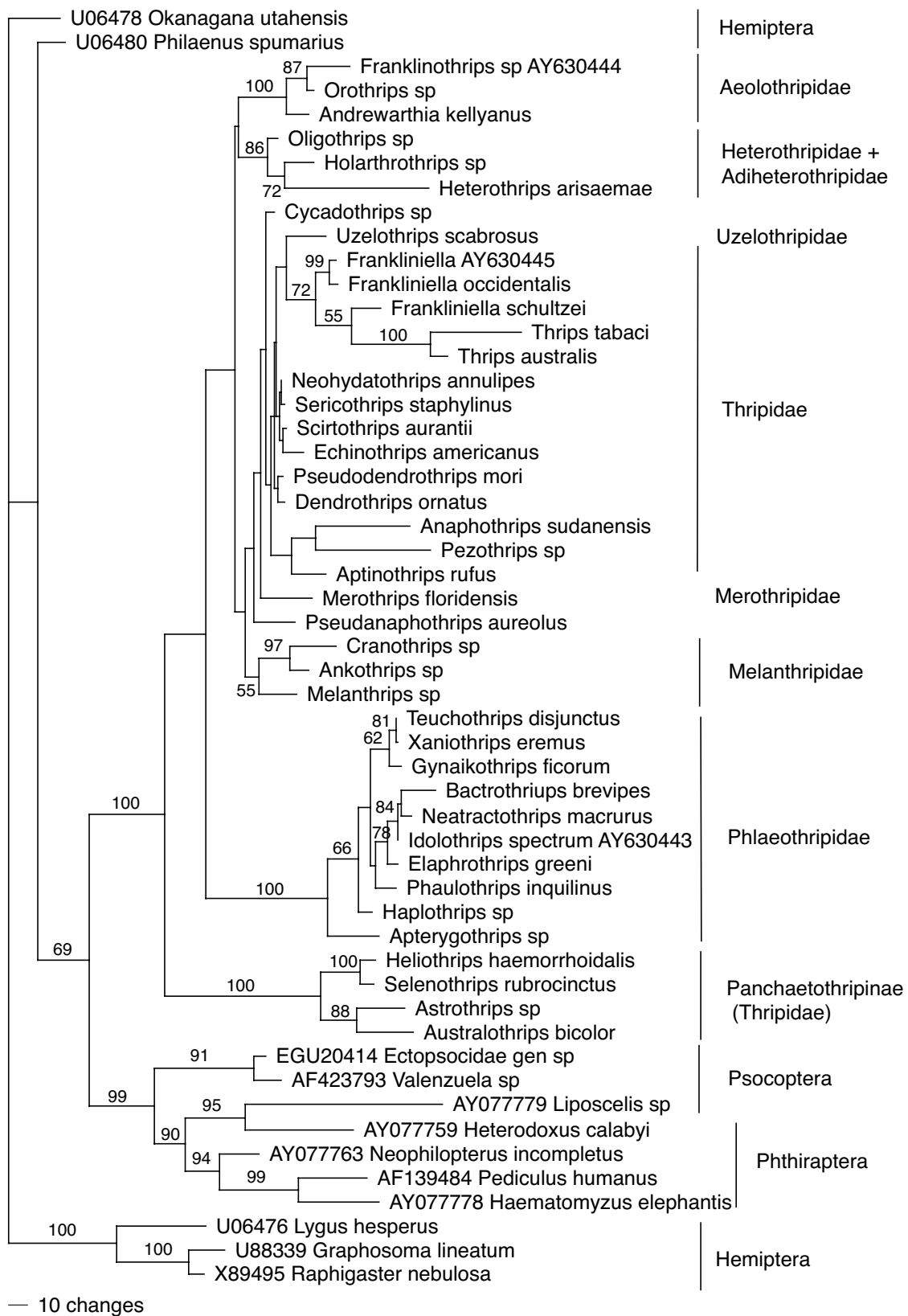
FIGURE 5. Phylogram resulting from analysis of 18S rDNA: one of two trees resulting from Parsimony analysis of data, numbers on branches indicate bootstrap proportions.
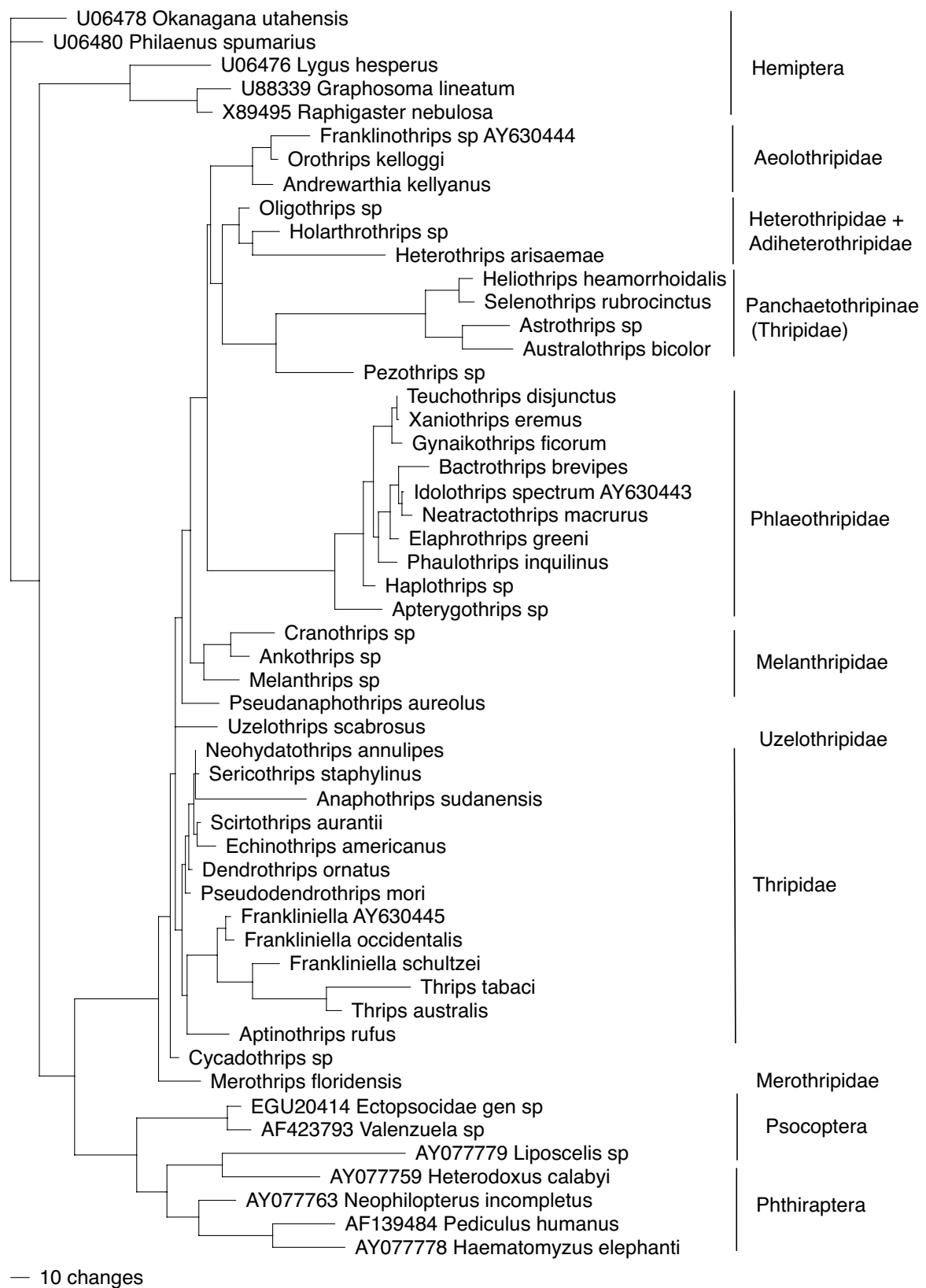
FIGURE 6. Phylogram resulting from maximum likelihood analysis of 18S rDNA data using a GTR + G + I model.

While these results provide some information on thysanopteran phylogeny, and some support for aspects of the existing classification, clearly far more resolution is required. Ideally more sequence data, for more taxa and from other gene regions, are necessary to construct an adequate hypothesis of relationships within this order. At this stage some areas of the taxon sampling are still weak (e.g. the larger families Thripidae and Phlaeothripidae) and require more taxa in order to test hypotheses of sub-family and tribal classifications. However, a more critical concern may be the lack of informative data at the base of the thysanopteran clade. While this area of research is ongoing, with some of the above concerns being addressed, there remains a need for informative low-copy nuclear genes to be explored to produce the data that may resolve the more ancient relationships within this somewhat enigmatic order.

Acknowledgements

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