The *Thrips* and *Frankliniella* genus-groups: the phylogenetic significance of ctenidia

Laurence A. Mound
CSIRO Entomology, P.O.Box 1700, Canberra, ACT 2601, Australia
E-mail: laurence.mound@csiro.au

Abstract: The two largest groups of species in the Thripidae, the *Thrips* and *Frankliniella* genus-groups, are not closely related, judging from the different chaetotaxy of the abdomen and head. The *Thrips* group is a lineage of species that apparently evolved in the Old World. In contrast, the *Frankliniella* group appears to be much older, possibly Gondwanan in origin, with independent diversifications into the South American and the S.E. Asian/Australian regions. Two new synonyms and one new combination are recognised amongst the Australian members of the *Frankliniella* group: *Parabaliothrips montanus* (Girault) [=*Pseudanaphothrips annettae* Mound & Palmer]; *Pseudanaphothrips aureolus* (Girault) **[=***Isochaetothrips melanurus* Steele].

Introduction

Taxonomy provides two essential outputs that support all other biological studies: 1, the discrimination of those inter-breeding groups that we call species, and 2, the classification of species into a system that reflects their evolutionary relationships. Tospovirus workers, for example, need to distinguish thrips vectors from non-vector species and, when considering the evolution of these viruses, they need to know the probable evolutionary relationships between the thrips vectors. Thysanoptera taxonomy has advanced considerably during the past 30 years, in particularly in our recognition of intraspecific variation. Studies of multiple samples of particular species have led to the recognition of many synonyms amongst the Thripidae (eg. Strassen 1996, 2000), and physical explanations for some of this variation are becoming available (Murai, 2002, this volume). Similarly, amongst Phlaeothripidae remarkable intra-specific polymorphisms have been recognised (eg. Palmer & Mound, 1978), and behavioural studies of intra-population competition have established an understanding of why such extreme structural variation occurs within some species (Crespi, 1986; Crespi & Mound, 1997).

In contrast, attempts at producing a classification that reflects evolutionary relationships have been much less successful. This is of particular concern when considering the subfamily Thripinae in which most pest thrips, and all the vectors of tospoviruses, are placed. Currently the Thripidae comprises four sub-families and a total of about 260 genera. However, three of these sub-families include a total of no more than about 55 genera (Panchaetothripinae with 35, Dendrothripinae and Sericothripinae each with about 10). Thus the Thripinae includes more than 200 genera, but with a supra-generic (Tribal or Sub-tribal) classification that is neither practical nor a reflection of relationships. For example, the "Chirothripini" represents a group of grass-living species that cannot be defined on any clear apomorphy, and the "Anaphothripina" has been used for a series of species whose only common characteristic is the lack of any long setae on the pronotum.

Amongst the Thripinae, almost 50% of the 200 genera each include just one species, with a further 40 each including only two species, 50 genera each have less than 10 species, and less than 30 genera include more than 10 species each. Thus, only six genera of Thripinae include more than 50 species each. This high proportion of small and monobasic genera results in a classification with little information about evolutionary relationships. Recognising this, Mound & Palmer (1981) attempted to define a series of 'genus-groups', drawing together some of the thripine genera into assemblages, although some of the groups they recognised

remain weakly defined. However, the two genus-groups based around *Frankliniella* and *Thrips* are particularly significant. Both can be defined by an apparently unique apomorphy, the presence of abdominal ctenidia, and these two groups are important because they include most of the recognised pest species.

Abdominal ctenidia

Ctenidia are paired structures, found laterally on abdominal tergites five (rarely four) to eight, and comprising an oblique row of equally sized and evenly spaced microtrichia arising from a single line of sculpture. These structures are essentially similar in appearance in all members of *Frankliniella* and *Thrips*, and a preliminary assumption would be that they are homologous in these two genera. That is, the presence of ctenidia may constitute a synapomorphy indicating that these two genera are closely related, and the two genus-groups are sister-groups. However, Mound & Palmer (1981) indicated that this assumption is not necessarily valid, Sakimura & O'Neill (1979) having emphasised the difference in position, and thus the possible non-homology, of ctenidia in the species of *Thrips* and *Frankliniella*.

Species of many genera of Thripinae have a patch of irregular microtrichia laterally on the tergites, particularly anterolateral to the spiracles on tergite VIII. Ctenidia appear to be derived from these lateral groups of tergal microtrichia, and members of the genus *Pseudanaphothrips* exhibit various stages in the organisation of ctenidia from irregular patches of microtrichia. There is thus no *a priori* reason for assuming that ctenidia had a single evolutionary origin. Indeed, essentially similar structures are present, presumably developed independently, in the unrelated Caribbean genus *Chaetisothrips*. Functionally, ctenidia appear to be associated with retaining the wings in the resting position dorso-laterally on the abdomen. If this is so, then the advantages of the ctenidiate condition are likely to impose considerable selection pressures, thus increasing the possibility of homoplasy. The objective of this study was therefore to examine the precise relationships of ctenidia to the tergal setae in representatives of all genera in the *Thrips* and *Frankliniella* groups, to evaluate the use of these structures for indicating systematic relationships.

Thrips genus-group

Mound & Palmer (1981) listed a series of genera in this group and, allowing for subsequent synonymies (Bhatti & Mound, 1981), the 14 genera are: *Baliothrips*, *Bolacothrips*, *Bournierothrips*, *Ctenidothrips*, *Ernothrips*, *Fulmekiola*, *Larothrips*, *Microcephalothrips*, *Rhinothripiella*, *Sphaeropothrips*, *Stenchaetothrips*, *Stenothrips*, *Thrips* and *Toxonothrips*. Members of these genera are remarkably consistent in the following character states:

1. head without a pair of setae anterior to first ocellus (ocellar setae pair I absent);
2. ctenidia on tergite VIII posterior to spiracles (Fig. 1);
3. ctenidia on tergites VI – VII terminate laterally at tergal discal setae S3 (Fig. 2);
4. tergites V – VII posteroangular seta arises near angle (Fig. 2);
5. tergites VI – VII discal setae S2 larger than S1& S3 (Fig. 2);
6. tergite VIII discal setae S1 & S2 subequal, larger than the small S3 (Fig 1);
7. ctenidia on tergite V terminate laterally posteromesad to setae S3

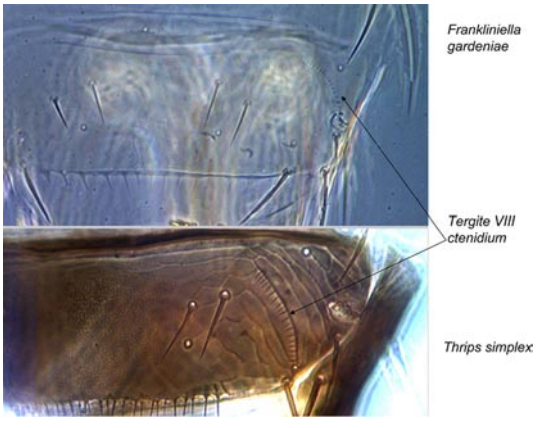

Fig. 1. Tergite VIII in *Thrips* and *Frankliniella*.

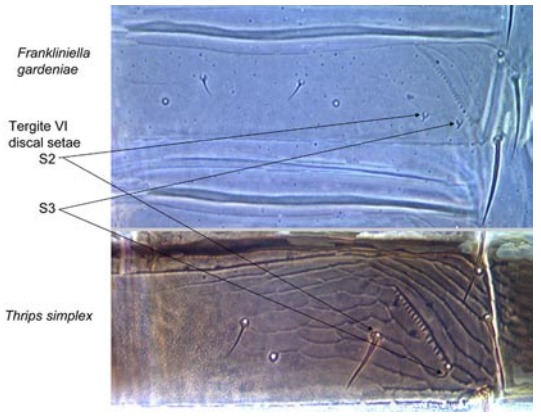

Fig. 2. Tergite VI in *Thrips* and *Frankliniella*.

Several genera in *Thrips* genus group include a single species, and there can be little doubt that recognition of these monobasic genera renders the genus *Thrips* paraphyletic. That is, each of the species, or species-groups, involved has evolved from within the genus *Thrips*, the structural differences presumably having evolved in response to particular environmental circumstances. Most of the species in these smaller genera live on the leaves of Poaceae. Thus, *Stenothrips* and *Baliothrips* represent three Palaearctic grass-living species that are, in effect, aberrant members of *Thrips* genus. Similarly *Stenchaetothrips*, *Ctenidothrips* and *Fulmekiola*, constitute an oriental lineage of *Thrips* species associated with grasses and bamboos, the single species allocated to each of the second and third of these genera having a distinctive toothed craspedum on the abdominal sternites. *Bolacothrips* is another Old World lineage with similar host associations, and *Toxonothrips* is known from one (or possibly two) species on Poaceae in western North America.

Sphaeropothrips includes a single Eurasian species that is probably associated with Cyperaceae, with the abdominal chaetotaxy similar to *Thrips* species but the chaetotaxy of antennal segment II slightly different. *Ernothrips* was based on a single female from grasses in India, and unlike the other members of the group has the ctenidia on tergite V terminating laterally at setae S3; the sternites bear a posteromarginal craspedum. In contrast, *Microcephalothrips* includes a single species that lives in Asteraceae flowers, and *Larothrips* a single African species that breeds in *Dioscorea* flowers. Also from Africa, *Bournierothrips* comprises five species from mosses that are distinguished from other members of this group by the lack of ocellar setae pair II as well as pair I. The only species in *Rhinothripiella*, from *Artemisia* on one of the Madeira Islands, has a long mouth cone and a toothed craspedum on the abdominal tergites, but is otherwise similar to *Thrips* species. Similarly, some authors recognise a genus *Isoneurothrips* for a single Australian species that has six rather than five setae on the vein of the forewing clavus. However, isolation of single species in this way does little to help us understand relationships within the *Thrips* lineage.

The consistency of form and position of the ctenidia and tergal setae throughout these species is so great that there can be little doubt that the species represent a single evolutionary lineage distinct from the rest of the Thripinae. This suggestion is supported independently by zoogeographical evidence, because no member of this entire lineage occurs naturally south of Mexico. Indeed, only one female of any *Thrips* species has ever been reported south of the United States southern border, apart from seven widespread species that are clearly introduced from other parts of the world (Nakahara, 1994). Two pest species of *Stenchaetothrips* are also introduced to South America from the Oriental Region (Mound & Marullo, 1996). From this geographic distribution we can deduce that the entire *Thrips* lineage has diversified relatively recently, since the separation of South America from the African continent. This is in sharp contrast to the situation in the *Frankliniella* genus-group.

Frankliniella genus-group

Mound & Palmer (1981) listed nine genera in this group: *Exophthalmothrips*, *Firmothrips*, *Frankliniella*, *Iridothrips*, *Kakothrips*, *Parabaliothrips*, *Pelikanothrips*, *Pseudanaphothrips* and *Sitothrips*, although *Exophthalmothrips* species are now considered aberrant members of *Frankliniella* (Mound and Marullo, 1996). All of the species in these

genera have the ctenidia on abdominal tergite VIII anterior to the spiracles (Fig. 1). Moreover, all but one of the species have a pair of setae on the head in front of the first ocellus (ocellar setae pair I), the sole exception being *Iridothrips mariae*. However, in contrast to the members of *Thrips* genus-group, considerable variation is present in the *Frankliniella* group in the form and position of the ctenidia and associated abdominal setae. Because of the variation between the genera in this group, a series of characters was evaluated, as indicated below.

It is interesting to note that in *Thrips* genus the chaetotaxy of the forewings is varied but that of the pronotum relatively constant, whereas in *Frankliniella* the reverse is true. Just as the presence of a complete row of setae on the first vein of the forewing is not a good indication of relationships within *Thrips*, so the absence of long setae on the anterior margin of the pronotum does not seem to be a good measure of relationship within *Frankliniella*. The *Frankliniella minuta* group, defined primarily by the absence of these long setae, is probably polyphyletic, as discussed further below.

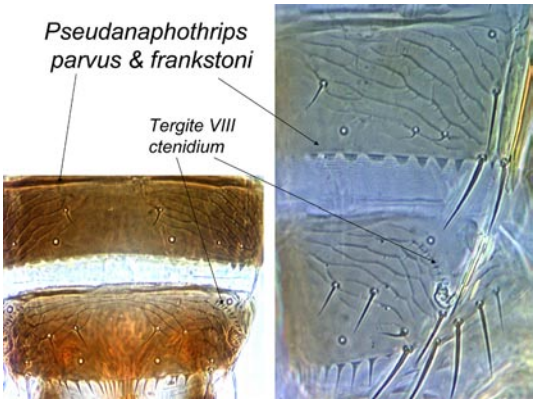

Fig. 3. Tergites VII - VIII in *Pseudanaphothrips*.

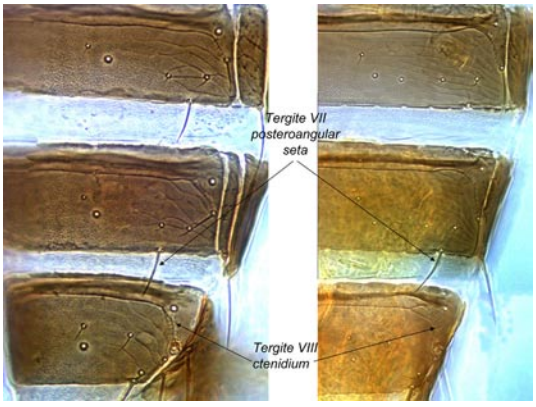

Fig. 4. Tergites VI - VIII in *Parabaliothrips*.

Character state evaluation

1. *Presence of a pair of setae anterior to first ocellus*: In Thripidae the head typically bears three pairs of setae in association with the ocelli. Ocellar setae pair I is the pair that is situated immediately in front of the first ocellus; pair II is usually situated laterally, close to the compound eyes; pair III varies in position but is commonly associated with the anterior margins of the ocellar triangle. Ocellar setae pair I is absent in all members of the *Thrips* genus group, but is present in all members of the *Frankliniella* genus group except *Iridothrips mariae*.

2. *Position of tergite VIII ctenidia relative to spiracles*: The plesiomorphic condition of microtrichia on tergite VIII involves an irregular patch anterior to the spiracles. As indicated above, members of the genus *Pseudanaphothrips* exhibit various stages in the organisation of ctenidia from irregular patches of microtrichia (Fig. 3). In members of *Frankliniella* genus group the ctenidia occupy the plesiomorphic position, anterior to the spiracles. However, in *Thrips* genus group the ctenidia are posterior to the spiracles, and this is possibly a more highly derived synapomorphy.

3. *Position of ctenidia on tergites VI – VII*: In *Pseudanaphothrips* species there are no ctenidia developed on tergites VI - VII. In members of the other genera, these ctenidia terminate laterally at one of three positions. For example, in *Thrips* species these ctenidia terminate at discal seta S3, in *Frankliniella* species they terminate just anterior to this seta, and in *Parabaliothrips* even further forward at the median lateral marginal seta.

4. *Position of posteroangular setae on tergites V – VII*: Abdominal tergites typically have one seta at, or close to, each posterior angle. In *Parabaliothrips*, and a few other taxa, these setae are displaced toward the mid line (Fig. 4).

5. *Relative size of discal setae S1 on tergites VI – VII*: In *Parabaliothrips* species, all three pairs of discal setae on tergites VI – VII are equally small. In contrast, in members of the *Frankliniella* genus group, setae S1 are usually larger than setae S2 and S3, whereas in *Thrips* genus group setae S1 are smaller than S2. 6. *Position of ocellar setae III relative to hind ocelli*: In most species of Thripidae, ocellar setae III arise in front of the tangent joining the anterior margins of the posterior ocelli. In many of the species considered here, these setae arise posterior to this tangent, between the posterior ocelli or even behind the ocelli. 7. *Pronotal posteromarginal median setae*: All but one species of *Frankliniella* have an extra pair of small setae medially between the usual median posteromarginal setae. This character state is also found in the species of *Sitothrips*, and also in *Pelikanothrips kratochvili* and *Iridothrips iridis*. 8. *Position of metanotal median pair of setae*: *Frankliniella* species always have the median pair of metanotal setae arising at the anterior margin of this sclerite, whereas in many members of *Thrips* genus this pair of setae arises behind the anterior margin. 9. *Metanotal sculpture*: *Parabaliothrips* species usually have the median area of the metanotum without any sculpture, whereas in *Frankliniella* species the sculpture is always transverse near the anterior margin and longitudinally reticulate medially. The sculpture in *Thrips* species is highly varied, from equiangular reticulate to striate. 10. *Tergite VIII posteromarginal comb*: The comb of microtrichia on the posterior margin of tergite VIII is used by thrips to help comb the fringe cilia of the wings into position. This comb is commonly not developed in members of *Thrips* and *Frankliniella* that have flightless adults, such as *Fr. antarctica* and *Fr. fusca*, also *T. discolor* and *T. difficilis*. However, there are other species that are always fully winged that also lack this comb, such as the common species *Fr. schultzei*, and some members of *Parabaliothrips*. 11. *Antennal segment III sense cone*: Most species of Thripidae have the major sense cone on this segment forked, but a few, often unrelated, species have this sense cone simple. 12. *Antennal segment IV sense cone*: Most species of Thripidae have the major sense cone on antennal segment IV forked, similar in form to that on segment III. Very few species have the sense cone differing in form between the two segments.

Analysis

The character matrix was analysed with Hennig-86, using the option ie, this producing a single tree (Fig. 5). This tree is poorly resolved, but *Kakothrips* was consistently associated with the species of *Parabaliothrips*, regardless of which option was chosen for the analysis, suggesting that *Kakothrips* has had

1. Ocellar setae I: present 0; absent 1;
2. Ctenidia on tergite VIII: anterior to spiracle 0; posterior to spiracle 1;
3. Ctenidia on tergites VI-VII: absent 0; ending at discal setae S3 1; ending anterior to discal setae S3 2; ending at median marginal seta 3;
4. Tergites V-VII posteroangular seta: close to angle 0; mesad of angle 1;
5. Tergites VI-VII discal setae S1: smaller than S2 0; larger than S2 1; as small as S2 2;
6. Ocellar setae III: anterior to tangent joining anterior margins of hind ocelli 0; posterior to tangent joining anterior margins of hind ocelli 1;
7. Pronotal posteromarginal median minor setae: absent 0; present 1;
8. Metanotal median setae: at anterior margin 0; behind anterior margin 1;
9. Metanotal sculpture: absent 0; longitudinal 1; transversely and longitudinally reticulate 2; equiangular reticulate 3;
10. Tergite VIII posteromarginal comb: present 0; absent 1;
11. Antennal segment III sense cone: forked 0; simple 1;
12. Antennal segment IV sense cone: forked 0; simple 1;

Table 1. Data matrix

	1	2	3	4	5	6	7	8	9	10	11	12
Thrips	1	1	1	0	0	0	0	1	1	0	0	0
Firmothrips	0	0	0	1	1	1	0	0	2	1	0	0
Frankliniella	0	0	2	0	1	0	1	0	2	0	0	0
Frankliniella schultzei	0	0	2	0	1	1	1	0	2	1	0	0
Iridothrips iridis	0	0	2	0	1	0	1	0	3	1	0	1
Iridothrips mariae	1	0	2	0	1	0	0	1	2	0	1	1
Kakothrips pisivorus	0	0	3	1	1	1	0	0	2	1	0	0
Parabaliothrips [Australian]	0	0	3	1	2	1	0	0	0	1	0	0
Parabaliothrips [Oriental]	0	0	3	1	2	1	0	0	0	0	0	0
Pelikanothrips	0	0	2	0	1	0	1	0	2	1	0	0
Pseudanaphothrips montanus	0	0	3	1	2	1	0	0	3	1	0	0
Pseudanaphothrips	0	0	0	0	1	1	0	0	1	0	0	0
Sitothrips	0	0	2	0	1	1	1	0	2	1	0	0

Table 2. Character State Matrix

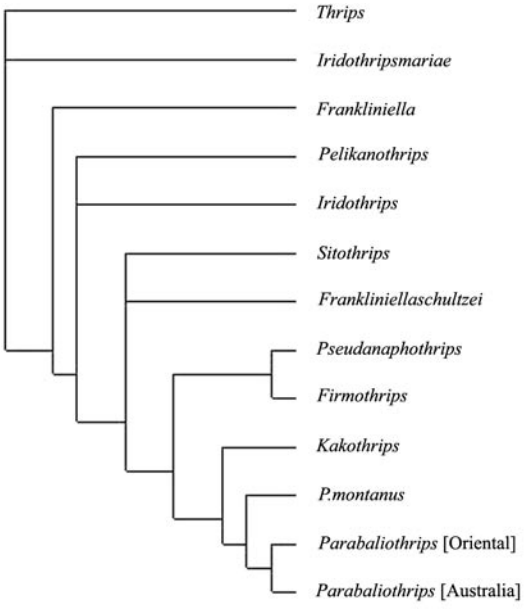

Fig. 5. Relationships within *Frankliniella* genus-group

a different derivation from other European members of the *Frankliniella* group. Moreover, the Australian species, *Pseudanaphothrips montanus*, groups with *Parabaliothrips*, even when the Australian and Oriental members of that genus are scored separately.

F. schultzei was added to the matrix as one example of the variation that occurs within the genus *Frankliniella*, this species both lacking a comb on tergite VIII and having ocellar setae III arising between the hind ocelli. As a result, the analysis fails to distinguish satisfactorily between the four genera, *Frankliniella*, *Iridothrips*, *Pelikanothrips* and *Sitothrips*. Moreover, the association between the Australian genus *Pseudanaphothrips* and the European genus *Sitothrips* is only weakly supported. Finally, *Iridothrips mariae* separates from all of the other members of the *Frankliniella* group.

Discussion

Frankliniella genus-group, in the narrow sense, thus comprises only four genera. *Sitothrips* species lack elongate setae on the anterior margin of the pronotum, but this may not be a good indicator of relationships. At least 30 neotropical species of *Frankliniella*, in the so-called *minuta*-group, also lack elongate setae on the anterior margin of the pronotum, but judging from variation in the ocellar chaetotaxy amongst these 30 species (Sakimura and O'Neill, 1979), they do not form a single evolutionary lineage. Thus, loss of elongate pronotal anteromarginal setae has probably arisen more than once within the genus *Frankliniella*. *Sitothrips* species have the setae on the forewing first vein widely spaced, but the genus is probably derived from *Frankliniella*, with the four members of the genus specialised for living on Poaceae. *Pelikanothrips* includes a single short winged species, and this also has short setae on the anterior margin of the pronotum. This species seems likely to have been derived from within *Frankliniella*, and a further possibly related species is *Frankliniella zizaniophylla* Han, from China. The fourth genus in this group, *Iridothrips*, also includes a single species, again

commonly short-winged. In contrast to the species of *Sitothrips* and *Pelikanothrips*, all of which have the head elongate, *I. iridis* has the head broad and produced in front of the eyes. Moreover, the sense cone on antennal segment III is simple although that on IV is forked. In contrast, *Iridothrips mariae* is probably unrelated to *I. iridis*, and presumably requires a new genus. Not only is ocellar setae pair I not developed, but the metanotal median setae arise well behind the anterior margin of this sclerite, and the pronotum lacks the pair of posteromedian minor setae.

The association between *Firmothrips* and *Pseudanaphothrips* indicated by the analysis is probably an artefact, caused by the fact that these are the only taxa in the group that lack ctenidia on tergites VI and VII. *Firmothrips* does not seem to be closely associated with *Frankliniella*, but is more likely to be related to *Kakothrips*. In this data matrix, *Kakothrips* is represented by the type species of the genus, *K. pisivorus*. Of the other four species currently included under this generic name, *K. dolosus* Berzosa was illustrated as having the pronotal median marginal setae present as in typical of *Frankliniella*. Unfortunately, there is no modern diagnosis of the genus *Kakothrips*, and three of the included species are possibly not closely related to *K. pisivorus*. The males of this species have the spiracles on tergite VIII arising on the posterior margin of a pair of curved tubercles, with the ctenidia along the leading edge of these tubercles. The association in the analysis of *Kakothrips* with *Parabaliothrips* suggests that the European genus may have been derived with this eastern genus rather than from *Frankliniella* in the west.

Parabaliothrips is a genus of leaf-feeding species found between Nepal and eastern Australia on a range of trees and shrubs. The genus has been revised recently, and an account given of the unusual mating system in one species that involves male leks (Gillespie *et al*., 2002). The genus is clearly distinct from most other members of the *Frankliniella* group, in that the ctenidia on tergites VI and VII end laterally at the median marginal seta (Fig. 4), as in *Kakothrips pisivorus*. The association of *Pseudanaphothrips montanus* with *Parabaliothrips* appears to be well supported in this analysis. Within *Pseudanaphothrips* it is aberrant, in that it has no posteromarginal comb on tergite VIII (Fig. 4), very weak sculpture on tergites IV – VIII, the tergal posteroangular setae arising mesad behind tergal discal setae S2 or S3, and the ctenidia on tergites VI – VII terminate laterally near the median marginal seta. However, the indication given by the above analysis that this species is related to the species of *Parabaliothrips* is accepted, with the nomenclatural conclusions indicated in Table 3. *P. montanus* was described on two females from Australia, and the synonym indicated in Table 3 on a series of specimens from New Zealand. It differs from the other members of *Parabaliothrips* in having antennal segment IV brown not yellow, the setae on the forewing veins widely spaced, and the metanotum with weak reticulate sculpture medially.

The genus *Pseudanaphothrips* now includes 10 Australian species, plus one species described on a single female apparently from Taiwan, and the ctenidia exhibit different levels of development amongst these species. In the type species, *P. achaetus*, the ctenidia on tergite VIII are usually,

***Parabaliothrips montanus* (Girault) comb.n.**
Physothrips montanus Girault, 1927: 1.
Pseudanaphothrips montanus (Girault); Mound and Houston, 1987: 7.
Pseudanaphothrips annettae Mound & Palmer, 1981: 166. **Syn.n.**

Pseudanaphothrips aureolus (Girault)
Physothrips aureolus Girault, 1928: 3.
Pseudanaphothrips aureolus (Girault); Mound and Houston, 1987: 7.
Isochaetothrips melanurus Steele, 1940: 328. **Syn.n**.

Table 3. Nomenclatural changes

but not always, well defined, and posteromesad of the spiracles there are two or three rows of microtrichia on the lines of sculpture. Thus, even within this single species the form of the ctenidia is not constant. Six further members of this genus have been studied, *P. araucariae*, *P. aureolus, P. casuarinae*, *P. frankstoni*, *P. pallidus* and *P. parvus*. In each of these there are clearly defined ctenidia anterolateral to the spiracles on tergite VIII, although sometimes with a few irregular microtrichia posteromesad to the spiracles. However, laterally on tergites VI – VII defined ctenidia are not developed, each of these species bearing about four rows of rather irregular microtrichia on the sculpture lines. At species level, some members of the genus cannot be distinguished satisfactorily (Palmer and Mound, 1981), but *P. aureolus* is a pale species with a distinctively elongate and dark tenth abdominal tergite. It was described from two females, and the synonymic species indicated in Table 3 from several females, but appears to be widespread in S.E. Australia on shrubby Asteraceae such as *Olearia* and *Cassinia*.

Conclusions

There is no evidence that the *Thrips* genus group shares a recent common ancestor with the *Frankliniella* genus group. The available evidence, both morphological and biogeographical, suggests that the *Thrips* group originated independently, apparently in the Old World after the separation of Africa from South America but before the North American and European landmasses had lost contact. Currently there is no good evidence indicating a sister taxon for this large group of species. In contrast, the *Frankliniella* group appears to be much older, possibly with a Gondwanan origin followed by subsequent spread into the northern hemisphere, both along the eastern and western routes but apparently not involving Africa.

References

Bhatti JS and Mound LA. 1981. The genera of grass and cereal-feeding Thysanoptera related to the genus *Thrips* (Thysanoptera: Thripidae). *Bulletin of Entomology* **21**(1980), 1-22.

Crespi BJ. 1986. Size assessment and alternative fighting tactics in *Elaphrothrips tuberculatus* (Insecta: Thysanoptera). *Animal Behaviour* **34**, 1324-1335.

Crespi BJ and Mound LA. 1997. Ecology and evolution of social behaviour among Australian gall thrips and their allies.166-180. In Choe, J. & Crespi, BJ (eds) *Evolution of Social Behaviour in Insects and Arachnids*. Cambridge University Press.

Gillespie PS, Mound LA and Wang C-L. 2002. Austro-oriental genus *Parabaliothrips* Priesner (Thysanoptera, Thripidae) with a new Australian species forming male aggregations. *Australian Journal of Entomology* **41**, 111-117.

Mound LA and Marullo R. 1996. The Thrips of Central and South America: An Introduction. *Memoirs on Entomology, International* **6**, 1-488.

Mound LA and Palmer JM. 1981. Phylogenetic relationships between some genera of Thripidae (Thysanoptera). *Entomologica Scandinavica* **15**, 153-17.

Nakahara S. 1994. The genus *Thrips* Linnaeus (Thysanoptera: Thripidae) of the New World. *United States Department of Agriculture. Technical Bulletin* **1822**, 1-183.

Palmer JM and Mound LA 1978. Nine genera of fungus-feeding Phlaeothripidae (Thysanoptera) from the Oriental Region. *Bulletin of the British Museum (Natural History)*. Ent. **37**, 153-215.

Sakimura K and O'Neill K. 1979. *Frankliniella*, redefinition of genus and revision of *minuta* group species (Thysanoptera: Thripidae). *U.S.Dept Agriculture, Technical Bulletin* **1572**, 1-49.

Zur Strassen R. 1996. Neue Daten zur Systematik und Verbrietung einiger west-palaarktischer Terebrantia-Arten (Thysanoptera). *Entomologische Nachrichten und Berichte* **40**, 111-118.

Zur Strassen R. 2000. Thysanopterologische Notizen (7) (Thysanoptera, Terebrantia). *Entomologische Nachrichten und Berichte* **44**, 25-34.