



## What is a genus—interpreting structural diversity among species of urothripine Phlaeothripinae (Thysanoptera)

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### Abstract

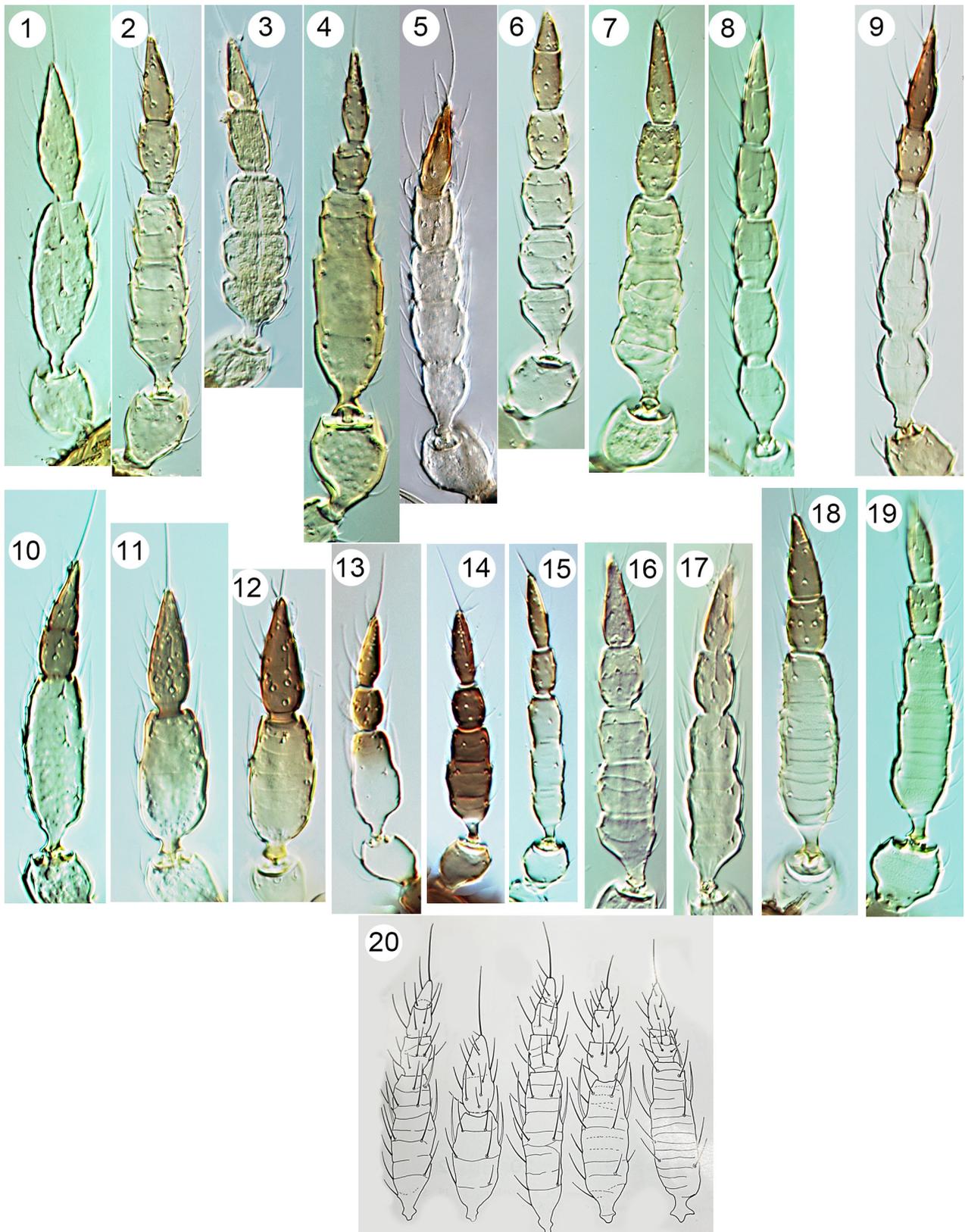
Variation within and between species is discussed in several obvious character states, including the number of visible antennal segments, prolongation of the anterior margin of the head, metaepimeral setae, and anal setae. As a result, *Bebelothrips* and *Conocephalothrips* are considered **new synonyms** of *Amphibolothrips*, and *Baenothrips* a **new synonym** of *Stephanothrips*. The revised generic classification suggests that urothripines are largely absent from the Neotropics, with four recorded species all likely to be introductions from the Old World.

**Key words:** variation, antennal segmentation, new synonymies, geographic distribution

### Introduction

A genus is an hypothesis, representing the opinion of one or more taxonomists concerning the structural relationships of a group of species, although it may be a single species that exhibits no character states that associate it with any pre-existing genus. As an hypothesis, a genus is subject to testing against new data, both structural or molecular, but it remains dependent on the interpretations and opinions of individual taxonomists. And a similar caveat applies to all taxonomic categories. Homoplasy amongst morphological features, the occurrence of similar states in species not closely related, is a recurrent problem in attempts to understand phylogenetic relationships within the insect order Thysanoptera (Minaei & Mound 2021). The generic classification of the urothripines, a worldwide group of mainly flightless species of Phlaeothripinae, reflects this issue. For this group of fungus feeding species, living mainly in leaf litter and at the base of grasses but sometimes on dead branches, most taxonomic studies have been based on small samples or even single specimens, and by various workers in different parts of the world.

This led to an emphasis on single unusual character states, autapomorphies, and thus the erection of many monobasic genera. Structural similarities amongst these genera resulted in Stannard (1952, 1957) synonymizing under *Amphibolothrips* the nine urothripine generic names that were available up to the 1950's. These synonymies proved unacceptable to other workers who, during the 1960's, added five further monobasic genera to the group. In response, Stannard (1970) re-validated the 15 genera by then available, added two further new genera, and attempted to re-evaluate their relationships. However, his illustrated “phylogenetic tree” of the 17 genera was of limited evolutionary significance, not being based on a phylogenetic framework, and some of the quoted geographical distributions are now considered incorrect. The next attempt to rationalize this generic classification (Mound 1972) included synonymizing four genera under *Baenothrips*. Subsequently, two further genera were synonymized under *Urothrips* by Ulitzka and Mound (2014), together with a discussion of some of the taxonomic problems associated with this group. The only other major publication on this group accepted that generic classification and provided keys to 12 species in five urothripine genera recorded from China (Tong & Zhao 2017).



**FIGURES 1–20.** Antennae of urothripines. (1) *Amphibolothrips grassii*; (2) *A. knechteli*; (3) *Conocephalothrips tricolor*; (4) *Bebelothrips flavicinctus*; (5) *Baenothrips guatemalensis*; (6) *B. moundsi*; (7) *B. chiliensis*; (8) *B. cuneatus*; (9) *Bradythrips hesperus*; (10) *Stephanothrips buffai*; (11) *S. uvarovi* (paratype); (12) *S. uvarovi* (Brazil); (13) *S. howei*; (14) *S. barretti*; (15) *S. broomei*; (16–17) *S. erythrinus* (paratypes); (18) *S. austrinus*; (19) *S. adnatus*; (20) Antennae of five Asian *Stephanothrips* species in Okajima (1989).

The generic classification of urothripines is re-opened here because several other genera seem equally poorly supported. In particular, *Baenothrips* is currently distinguished from *Stephanothrips* on the grounds that antennal segments III–V are either separate from each other or are fused into a single unit. But when every described species is considered, these two conditions are by no means distinct (Fig 5–19). Moreover, the fusion of antennal segments does not seem to be closely correlated with any other character states. For example, although several species placed in *Baenothrips* have a pair of prominent setae laterally on the metaepimera, including the type species *guatemalensis*, other species placed in that genus lack these setae, as do all of the species placed in *Stephanothrips*. The situation becomes even more confusing when considering the polarity of such character states, leading to the conclusion that some states have been subject to reversal.

The objectives here are to review the various attempts at generic classification of urothripines, to discuss patterns of variation in this group in several characters, to place three further generic names into synonymy, to present a new identification key to the seven genera of urothripines accepted here, and to look for correlations between these genera and their geographical distributions.

## Character state variation

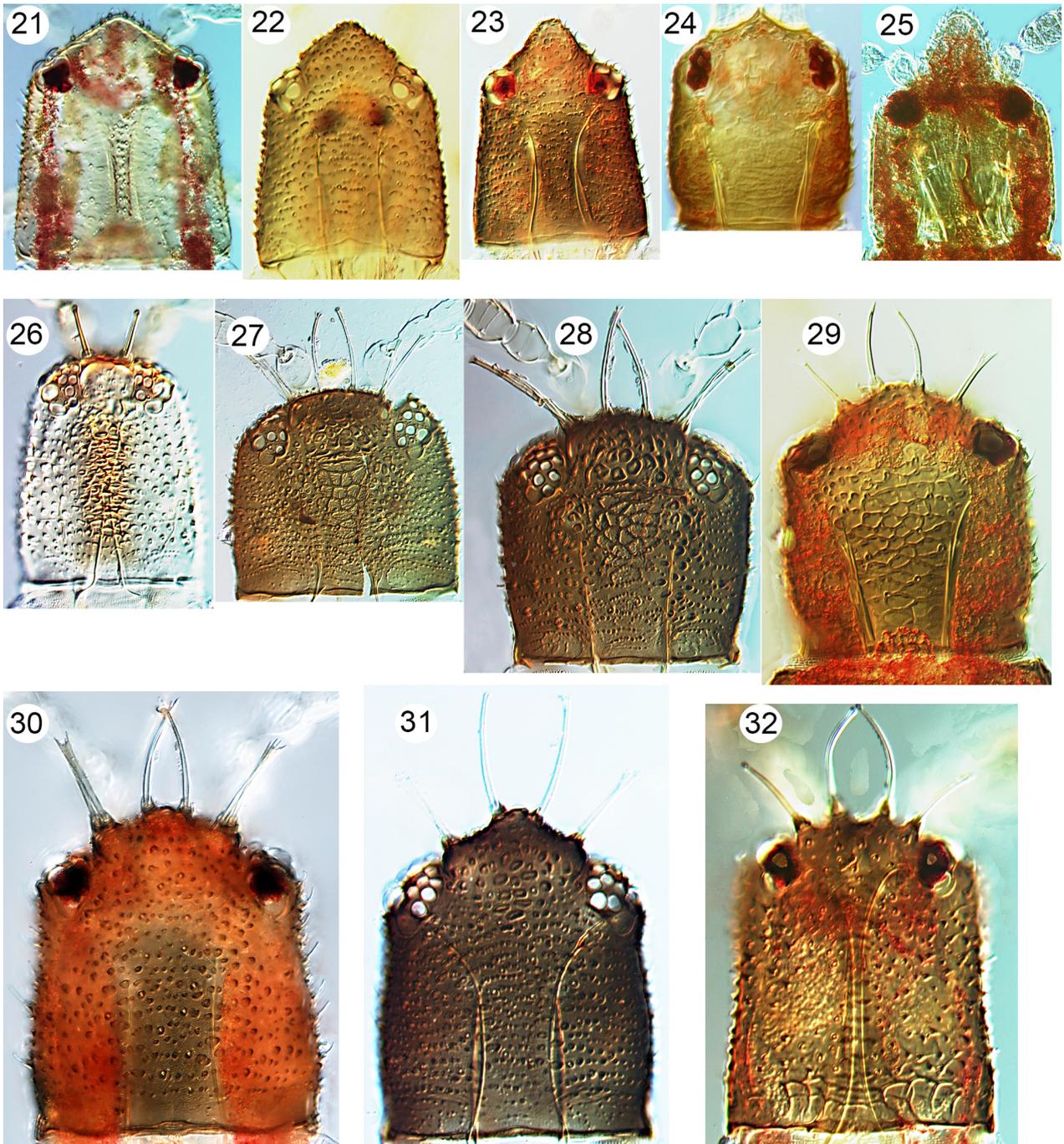
*Antennal segmentation:* Okajima (1989) described five new species of *Stephanothrips* from parts of Malaysia and Indonesia, and his published illustration of their different antennae is reproduced here (Fig. 20). One species has antennae similar to that of the type species of the genus, *S. buffai* from South Africa, with segments III–V completely fused, and VI–VIII fused but with a faint transverse line ventrally. In the other four species, segment V is sometimes weakly indicated but in each one VI is distinct, with VII fused to VIII only in one species. However, in Australia a similar condition with antennal segments III–V completely fused occurs in *S. howei* with *S. barretti* showing an intermediate condition (Figs 10–14). Similar patterns of variation in the extent of fusion occur amongst the species here placed in *Amphibolothrips* (Figs 1–4), as well as those in *Urothrips*. The two species placed in the genera *Habrothrips* and *Octurothrips* have retained the plesiomorphic antennal condition of eight free segments (Figs 40, 43). Among the other urothripines, fusion between antennal segments is not only a derived condition, it has occurred convergently on multiple occasions, as indicated in Figures 1–20. As a result of the unstable visible antennal segmentation in this lineage, the number of antennal segments is here considered too variable to provide a useful distinction at genus level.

*Head projection:* Five species are here considered to be members of *Amphibolothrips*, and four of these have the vertex projecting over the bases of the antennae. Similarly, among the seven species of *Urothrips* the vertex projects in three species, although in most members of the urothripine group this condition is not found. The head projection of *Habrothrips* is not homologous because the antennae arise at the apex (Fig. 40).

*Cephalic setae:* Almost two-thirds of the 81 species currently listed in this group have one to three pairs of prominent setae on the anterior margin of the vertex (Figs 26–32), and all of these species are here placed in the genera *Bradythrips* and *Stephanothrips* (plus *Baenothrips*). The most common condition is the presence of three pairs of these setae, one pair close to the midline and two pairs closer to the eyes, and logically this is likely to be the most highly derived condition. The length of these setae varies greatly between species, one *Stephanothrips* species lacks the median setal pair, and the six species of *Bradythrips* have only the median pair and not the lateral pairs. This is discussed further below, because complete absence of these setae may not be an independent state but merely part of a series from zero to three.

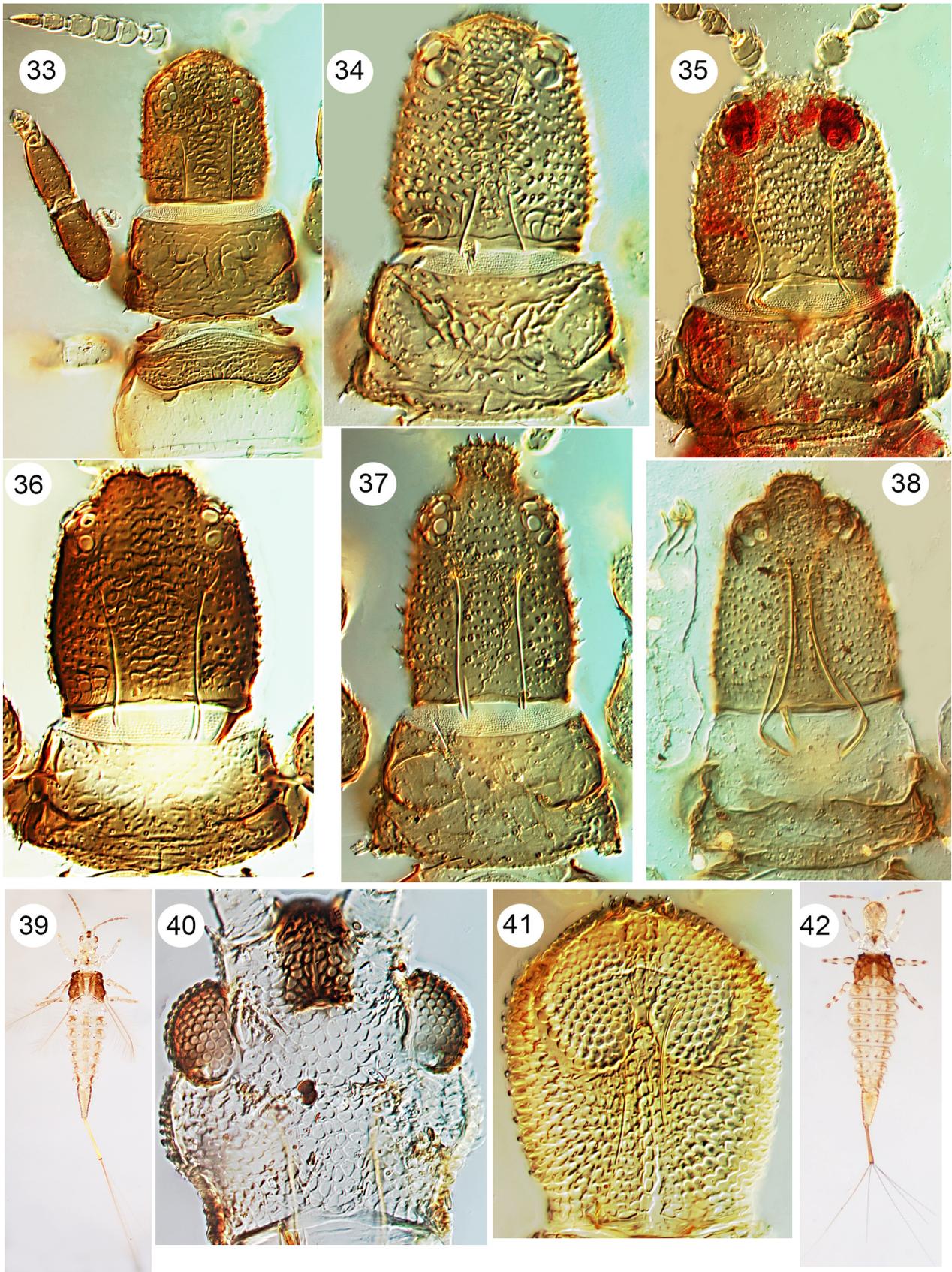
*Fore tarsal hamus:* The two species in *Habrothrips* and *Octurothrips* have a hamus on the fore tarsus similar to that found widely amongst Phlaeothripidae, projecting ventro-medially. In contrast, all except one of the 12 *Urothrips* species have a hamus that projects laterally on the external margin of each fore tarsus. A similar external lateral hamus is found in the widespread species *Stephanothrips occidentalis*, and this condition is considered further below under relationships.

*Metaepimeral setae:* These setae are prominent laterally in *Habrothrips* and *Octurothrips*, the two genera that have retained the plesiomorphic condition of the antennae. These setae are also prominent in the type species of *Baenothrips* as well as in at least six other species previously placed in that genus. However, they are not present in four species placed in *Baenothrips* from Australia, nor in one from India. Prominent metaepimeral setae do not occur in any other member of the urothripine group, although the type species of *Bradythrips* has a small pair of apparently homologous setae in this position.



**FIGURES 21–32.** Heads of urothripines. (21) *Amphibolothrips grassii*; (22) *A. knechteli*; (23) *A. marginatus*; (24) *Bebelothrips flavicinctus*; (25) *Conocephalothrips tricolor*; (26) *Bradythrips hesperus*; (27) *Baenothrips cuneatus*; (28) *B. murphyi*; (29) *S. erythrinus*; (30) *B. guatemalensis*; (31) *B. moundi*; (32) *Stephanothrips uvarovi* [paratype].

*Anal setae:* Species in this group typically have three pairs of very long setae at the apex of the tenth tergite, the tube (Figs 39, 42). However, the mid-dorsal pair is often rather shorter than the other two pairs. In one species from Australia, *bulbosus*, this pair is scarcely 0.3 as long as the two lateral pairs, and in *caenosus* the median dorsal pair of setae is represented by minute papillae. Even more remarkably, in *tricolor* from Hawaii these setae are flattened and scale-like, and less than 10 microns long.



**FIGURES 33–42.** Heads of urothripines. (33) *Urothrips paradoxus*; (34) *U. calvus*; (35) *U. tarai*; (36) *U. reedi*; (37) *U. junctus*; (38) *U. probolus*. (39–40) *Habrothrips curiosus*. (41–42) *Octurothrips pulcher*.

## Generic relationships

In the key to genera below the first three genera seem to be fully distinct. However, couplet 4 relies on the presence/absence of cephalic setae as being independent states, and as indicated above this is not entirely logical. *Urothrips calvus* lacks a fore tarsal hamus and could equally well be considered a species of *Stephanothrips* that lacks cephalic setae. And the available specimens of *Amphibolothrips* are all slide mounted in such a manner that “absence” of a fore tarsal hamus may be due to an inability to see such a small structure. As a result, the final four genera in the key remain less than satisfactorily diagnosed from each other, and are retained here with considerable doubts. The only published molecular data on urothripines (Buckman *et al.* 2013) resolved the only available species as external to all other Phlaeothripidae, despite the morphological structures suggesting a more highly derived group of species.

## Geographic distributions

The generic classification of the urothripines presented here suggests some interesting geographic distributions. *Amphibolothrips*, as treated below, is southern Palaearctic in distribution, but with *tricolor* known only from two specimens taken at Oahu on the Hawaiian Islands. In the absence of further specimens, it is not possible to know if *tricolor* is native to those islands, or if it has been introduced from the northern hemisphere. In contrast, *Trachythrips* is known only from the New World, although only one of the 11 species has been described from South America, the others being from Panama, the Caribbean Islands and southern USA.

The two genera that are interpreted as retaining most characters in a plesiomorphic state are the monobasic *Habrothrips* and *Octurothrips*. These two are both from the Old World, in eastern Asia and/or Australia, but do not seem to form a monophyletic sister-group to the other extant urothripines. Instead, based on their structural differences they may even be two independent basal lineages. *Urothrips* is also widespread across the Old World tropics, from Africa to Australia. The genus that is interpreted as having the most characters in the derived state, *Stephanothrips*, is by far the most species rich. These species have the derived condition of antennal segments III–V more or less fused (Figs 10–19), whereas in the closely related *Bradythrips* the plesiomorphic condition is retained with antennal segments III–V distinct from each other (Fig. 9). These two genera are here considered to be Old World, with the few species reported from the Neotropics in the genera *Baenothrips* and *Stephanothrips* considered below as more likely to have been introduced by human trading.

The single known specimen of *Baenothrips guatemalensis* was actually taken in quarantine at San Francisco, USA, in association with an orchid plant said to have been imported from Guatemala. Given the doubts accompanying such quarantine records, the country of origin of this thrips specimen remains uncertain. A closely similar species, *B. chiliensis*, has been seen in several samples from Chile where it is clearly established. However, both *chiliensis* and *guatemalensis* are remarkably similar in structure and sculpture to *B. moundi*, a species that is widespread in leaf-litter across the continent of Australia. We suggest that these three names are likely to refer to a single species that varies slightly in colour and in the degree of antennal fusion. This conclusion seems to be rather more likely than an alternative hypothesis of an independent radiation in South America. The third urothripine recorded exclusively from the Neotropics, *Stephanothrips erythrinus*, remains known only from the original specimens taken in Argentina at another site near the west coast of South America (Figs 16–17). This species shares most character states with some southeast Asian species listed in *Baenothrips* that have reticulate sculpture on the vertex, including *asper*, *minutus*, *murphii* and *ryukyuensis*. Again, this species has possibly been introduced from Asia rather than representing an independent Neotropical radiation. A fourth urothripine species taken in the Neotropics is a species of *Stephanothrips* known from two females taken by J.D. Hood in 1948 at two sites in Brazil in the state of São Paulo, and one female taken in 2011 at Porto Alegre in the state of Rio Grande de Sul. The latter specimen has been compared directly with specimens of two *Stephanothrips* species from southern Africa: *S. buffai* (identified by zur Strassen from Congo, South Kivu), and a paratype of *S. uvarovi* from Cape Province, South Africa (Figs 11–12). No significant differences could be found between the specimens from Brazil and *uvarovi*, they both have the pronotum and abdominal tergites bicoloured, and this again raises the question of Neotropical endemism or introduction. Considering the many studies on Thysanoptera of the Neotropics by J.D. Hood and D. Moulton, including extensive leaf-litter sampling (Mound 1977), it is remarkable how few specimens of this distinctive and interesting urothripine group have been reported from South America. This lack of collections provides no support

for any hypothesis that the urothripines have diversified independently in the Neotropics. In contrast, it lends further credence to the possibility that all four members of this group recorded from South America represent introductions from overseas.

The possible origins of such disrupted distributions of small insects were discussed by Mound (1970: 88) in connection with the ballast (and galley-fire wood) carried by the vast tonnage of sailing ships in the 18<sup>th</sup> and 19<sup>th</sup> centuries. Sailing ships had to be trimmed to float at a particular level in the water (the Plimsoll line), and this was achieved, only after the cargo was loaded, by adding or removing ballast to or from the “ballast quay” (Mound 1970, 1983). Biologists with an interest in distributions need to remember the extent of this sailing ship trade that lasted for over 300 years. Portugal had a vigorous trade with the Asian “spice islands”, with southeast Africa and with Brazil, and Britain had a similar extensive trading pattern. In east Africa, Germans imported and created a central European forest with imported plants in huge tubs of soil, and British settlers in Australia tried to make parts of that continent “look like home” through the activity of “acclimatisation societies”. It should not surprise us that many organisms, including weedy plants and insects, also some fungus-feeding thrips, survived such voyages to entirely new parts of the world.

### Distinguishing the Urothripine genera

- |    |   |                        |
|----|---|------------------------|
| 1. | Compound eyes each with at least 30 facets (Figs 40–41), all equal in size; antennal segment III slender, usually 3–4 times as long as wide and not narrowed sharply to base; mid and hind tarsi 2-segmented; fore tarsal hamus directed ventrally; metathoracic epimera each with a prominent lateral seta. . . . .  | 2                      |
| -. | Compound eyes never with more than 15 facets (Figs 27–28), some dorsal facets much larger than others; antennal segment III almost globose, scarcely 2 times as long as wide and sharply narrowed to basal stem (sometimes fused to segment IV or to IV+V); mid and hind tarsi 1-segmented; fore tarsal hamus, when present, directed laterally; metathoracic epimera with or without such a seta . . . . . | 3                      |
| 2. | Head projecting over bases of first antennal segment (Fig 41); eyes almost holoptic but with no facets ventrally; head with genae narrowing to base; prosternal basantra present and transverse . . . . .   | <i>Octurothrips</i>    |
| -. | Head projecting strongly in front of eyes with antennae arising at apex (Fig. 40); compound eyes globose on dorsal and ventral surfaces; head sharply narrowed to base; prosternal basantra reduced to weak sclerites placed anterolaterally. . . . .   | <i>Habrothrips</i>     |
| 3. | Prosternal basantra transverse across anterior margins of ferna. . . . .  | <i>Trachythrips</i>    |
| -. | Prosternal basantra absent or reduced to small anterolateral sclerites . . . . .  | 4                      |
| 4. | Anterior margin of head with prominent setae, rarely reduced to a single small pair (Figs 26–32) . . . . .  | 5                      |
| -. | Anterior margin of head with no prominent setae (Figs 33–38) . . . . .  | 6                      |
| 5. | Antennal segment III narrowed at apex and distinct from narrowed base of IV (Fig. 9); maxillary stylets close together medially in head . . . . .   | <i>Bradythrips</i>     |
| -. | Antennal segment III broad at apex and close to broad base of IV, segments III–V weakly to closely fused; maxillary stylets about 0.3 of head width apart. . . . .  | <i>Stephanothrips</i>  |
| 6. | Fore tarsus with hamus. . . . .   | <i>Urothrips</i>       |
| -. | Fore tarsal hamus absent . . . . .  | <i>Amphibolothrips</i> |

### *Amphibolothrips* Buffa

*Amphibolothrips* Buffa, 1909: 193. Type species *Amphibolothrips grassii* Buffa.

*Bebelothrips* Buffa, 1909: 195. Type species *Bebelothrips latus* Buffa. **Syn.n**

*Conocephalothrips* Bianchi, 1946: 499. Type species *Conocephalothrips tricolor* Bianchi. **Syn.n.**

Buffa (1909) erected this genus for a single species, *grassii*, based on a single specimen from Lake Albano near Rome, in Italy. This species is currently recorded also from southern France and Spain. In the same paper, Buffa also erected *Bebelothrips* for a single species, *latus*, based on three females from Isola del Giglio, an island between the west coast of Italy and Corsica. The original specimens of both species are currently not known to exist, however *Trachythrips flavicinctus* Bournier from southern France is now considered a synonym of *latus*. The genus *Bebelothrips* has remained distinguished from *Amphibolothrips* based only on the differing number of antennal segments (Priesner 1964). However, despite the larger number of antennal segments, Stannard (1970) transferred *Trachythrips marginatus* Bournier from southern France to *Amphibolothrips*, and Mound (1972) similarly transferred *Bebelothrips knechteli* Priesner, a species that is recorded only from Romania and the Canary Islands.

Bianchi (1946) erected *Conocephalothrips* for the single species *tricolor*, and this remains known only from

two females collected on Oahu. The new genus was compared only to *Urothrips* and no mention was made of *Amphibolothrips* although the head of *grassii*, the only species of the genus known at that time, is similarly produced forward over the antennal bases (Figs 21–25). The antennal segments of *grassii* are more extensively fused than in *tricolor*, in which antennal segments III–V are distinct but broadly joined (Figs 1–3). The antennae of *Bebelothrips latus*, and also of the other two species now placed in *Amphibolothrips*, are intermediate in structure between *grassii* and *tricolor*. The body of the holotype of *tricolor* has too much pigment for basantra to be visible, but the species is unusual in having the dorsal pair of anal setae flattened and scale-like, and less than 10 microns long.

It is not possible to know if the species *tricolor* is a natural inhabitant of the Hawaiian Islands, or if it has been introduced to Oahu from some other part of the world. In the northern part of North America almost nothing is known of the leaf litter thrips fauna, but the other four species here recognised in *Amphibolothrips* are all from the southern parts of Europe. However, despite the interpretation adopted here of the available data, there is a further problem in distinguishing *Amphibolothrips* from *Urothrips*. The distinction between these indicated above in the key to genera fails with just one of the 12 described species of *Urothrips*. The fore tarsal hamus of *calvus* from eastern China appears to be absent, although it is also very small in *lancangensis* from southern China.

The new synonymy of *Bebelothrips* and *Conocephalothrips* with *Amphibolothrips* results in two new combinations as listed in Table 1.

### ***Bradythrips* Hood & Williams**

*Bradythrips* Hood & Williams, in Hood, 1925: 68. Type species *Bradythrips hesperus* Hood & Williams.

The type species was based on a single wingless female collected in Guyana, on the north coast of South America. However, at the U.S. National Museum in Washington and in the collections of Universidade Federal do Piauí, Floriano, in Brazil, we have studied in addition to this holotype the following wingless females of *B. hesperus*: one from Panama, seven from Guyana, and more than 10 from Brazil along the Amazon River basin (States of Amazonas, Pará and Amapá). In contrast, the other five species that are now known in this genus are all from southeast Asia, including Malaysia, southern China, Philippines and Borneo, and specimens of *hesperus* have also been recorded from India, Borneo and the Solomon Islands (Okajima 1987). These records indicate that *Bradythrips* is likely to be a genus of the Asian tropics but with one species that has been inadvertently transported to South America, probably by sailing ships.

A key to five of the six species of *Bradythrips* is available (Okajima & Urushihara 1995a), and of the two species with the pronotum and fore legs yellow, *zhangii* differs from *hesperus* in having the head more uniformly brown and the abdominal tergites with narrow longitudinal sculpture medially. All six species have antennal segments III–V clearly distinct from each other, in contrast to the condition in *Stephanothrips* species. The members of *Bradythrips* differ from those previously placed in *Baenothrips* in having the maxillary stylets close together medially in the head, and only a single pair of prominent setae on the anterior margin of the head (Fig. 26). Although *B. hesperus* has the metathoracic epimera bearing a small stout seta laterally, it appears that the other members of this genus lack this structure.

### ***Habrothrips* Ananthkrishnan**

*Habrothrips* Ananthkrishnan, 1968: 137. Type species *Habrothrips curiosus* Ananthkrishnan.

The single species in this genus is widely distributed in leaf-litter between India and northern Australia, and all known specimens of both sexes are macropterae (Figs 39–40). It shares with other urothripine species the long abdominal segments IX–X and the presence of a pair of prominent setae on the metathoracic epimera, but it exhibits several unusual features. The following can probably be considered plesiomorphic: compound eyes large and globose, mid and hind tarsi 2-segmented, and fore tarsal hamus directed ventro-medially. However, the following character states are more highly derived, and are unique among urothripines: head strongly projecting in front of eyes, and abdominal tergites with a median groove bearing two pairs of leaf-like setae that are presumably wing-retaining.

## ***Octurothrips* Priesner**

*Octurothrips* Priesner, 1931: 93. Type species *Octurothrips pulcher* Priesner.

Known only from Australia, the single species in this genus has been found widely in the inland arid zone of the eastern part of this continent (Figs 41–42). Although all of the available specimens are apterae, the species shares many character states with *Habrothrips curiosus*, including the abdominal tergites with a groove down the midline. However, the head is remarkable with greatly enlarged, almost holoptic. compound eyes, with the genae extending forward laterally around the eyes, and the prosternal basantra large and transverse.

## ***Stephanothrips* Trybom**

*Stephanothrips* Trybom, 1912: 42. Type species *Stephanothrips buffai* Trybom.

*Baenothrips* Crawford, 1948: 39. Type species *Baenothrips guatemalensis* Crawford, **syn.n.**

*Verrucothrips* Stannard, 1952: 128. Type species *Amphibolothrips (Verrucothrips) caenosa* Stannard.

*Ramachandraiella* Ananthakrishnan, 1964: 228. Type species *Ramachandraiella minuta* Ananthakrishnan.

*Transithrips* Bournier, 1963: 81. Type species *Transithrips asper* Bournier.

*Bournieria* Ananthakrishnan, 1966: 2. Type species *Bournieria indica* Ananthakrishnan.

Four of the generic synonyms indicated above were discussed by Mound (1972: 92), but the validity of *Baenothrips* has not been questioned since Stannard (1952). The sole distinction between *Baenothrips* and *Stephanothrips* has been in the degree of separation between antennal segments III–V, being separate in the first genus but largely fused in the second. *Baenothrips guatemalensis*, the type species of that genus, is interpreted as having segments III–V distinct from each other (Fig. 5), although the separation between them is by no means clear. Among the various species placed in *Baenothrips* only *asper* and *cuneatus* have these segments clearly separate (Fig. 8). In the only known specimen of *guatemalensis* segments VII and VIII are fused with scarcely any trace of suture, and this is also true of *chiliensis* (Fig. 7). Very similar to these in structure and sculpture, the Australian species, *moundi*, has segment VIII clearly distinct (Fig. 6). A further problem is that in another Australian species, *B. caenosus*, antennal segments VII and VIII can be either fused or separate (Mound 1972). There is also a lack of clarity in distinctions between some described species. For example, Bhatti (2002) published a detailed morphological study of a paratype of *asper*, recognizing that specimens identified as *asper* from India do not represent that African species. The original illustration of *asper* by Bournier, as well as the illustrations of a paratype by Bhatti, indicate that, in this species from Angola, antennal segments III–V are clearly distinct from each other, much as in *cuneatus* (Fig. 8). In contrast, the antennae of Indian specimens labelled by Ananthakrishnan as *asper* (Ooty, vii.1970) have segments III–V broadly joined.

Our interpretation is that antennal segment fusion has been subject to several reversals among the various species, and that this character state cannot be employed to distinguish natural groups. As a result, the genus *Baenothrips* is here considered a synonym of *Stephanothrips*, and that genus will now include 47 species. These comprise 26 species from the Asian tropics, nine from Australia, three from Africa, and four from southern USA, plus four from South America where they are possibly introduced (see above Geographic considerations). In addition, because the only known males of *occidentalis* were taken in Thailand (Okajima & Urushihara 1995b), it is probable that this pantropical species is also Asian in origin. Since several of the nine species from Australia are known only from the northern subtropical parts of this continent, it is clear that the distribution of species in this genus is primarily in association with the southeast Asian tropics. The new synonymy of *Baenothrips* with *Stephanothrips* results in the 15 new combinations listed in Table 1.

## ***Trachythrips* Hood**

*Trachythrips* Hood, 1930: 317. Type species *Trachythrips watsoni* Hood.

Alone amongst the urothripine genera, the members of this genus have the pronotal basantra fully transverse across the anterior margins of the ferna, although the posterior margin of the basantra is not always fully sclerotised in

some of the specimens examined. This character state of the basantra, paralleling the geographical distribution of the genus, suggests a single New World radiation with the 11 members of the genus restricted to the American continent and Caribbean islands, between California, Texas, Florida and southern Brazil. Structurally similar to each other, the species of this genus apparently are all wingless, with some differing from others in little more than colour patterns.

## ***Urothrips* Bagnall**

*Urothrips* Bagnall, 1909: 126. Type species *Urothrips paradoxus* Bagnall.

*Coxothrips* Bournier, 1963: 75. Type species *Coxothrips reticulatus* Bournier. Synonymised by Ulitzka & Mound, 2014.

*Ananthakrishnaniella* Stannard, 1970: 118. Type species *Ananthakrishnaniella tarai* Stannard. Synonymised by Bhatti, 1998: 178.

*Biconothrips* Stannard, 1970: 121. Type species *Biconothrips reedi* Stannard. Synonymised by Ulitzka & Mound, 2014.

Within the key to genera of urothripines presented by Mound (1972), one group of four genera was distinguished by the following three character-states: absence of elongate setae on anterior margin of head; presence of prominent external fore tarsal hamus; reduction of prosternal basantra (=praepectus) to a pair of small triangles placed laterally. However, there is considerable overlap in character states amongst the nine species involved under these four generic names, and Ulitzka and Mound (2014) decided to include all nine species within a single genus, *Urothrips*. The alternative to accepting a single genus to encompass the range of variation amongst these species would be to recognise more than four monotypic genera, each of which would be supported by a single autapomorphy with no obvious systematic significance. The problem of distinguishing genera based on characters that seem to vary progressively in fusion or size increases when all 12 of the species now listed in *Urothrips* are considered. In one of these species, *U. lancangensis*, the fore tarsal hamus is very small, and in *U. calvus* it appears to be quite undeveloped. Similarly, the only available specimen of *U. bagnalli* Trybom is uncleaned but seems to have transverse basantra. At species level within the genus there appear to be further problems, in that populations of *paradoxus* in Africa differ in colour details, as is known amongst populations of *reedi* in Australia (Mound 1972).

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## **TABLE 1. Nomenclatural changes proposed here**

*Amphibolothrips latus* (Buffa, 1909) **comb. n.**

*Amphibolothrips tricolor* (Bianchi, 1946) **comb. n.**

*Stephanothrips asper* (Bournier, 1963) **comb. n.**

*Stephanothrips bulbosus* (Mound & Wells, 2023) **comb. n.**

*Stephanothrips caenosus* (Stannard, 1952) **comb. n.**

*Stephanothrips chiliensis* (Stannard, 1970) **comb. n.**

*Stephanothrips cuneatus* (Zhao & Tong, 2016) **comb. n.**

*Stephanothrips erythrinus* (Pelikán, 1964) **comb. n.**

*Stephanothrips goweri* (Mound & Wells, 2023) **comb. n.**

*Stephanothrips guatemalensis* (Crawford JC, 1948) **comb. n.**

*Stephanothrips indicus* (Ananthakrishnan, 1966) **comb. n.**  
*Stephanothrips leukos* (Mound & Wells, 2023) **comb. n.**  
*Stephanothrips minutus* (Ananthakrishnan, 1964) **comb. n.**  
*Stephanothrips moundi* (Stannard, 1970) **comb. n.**  
*Stephanothrips murphyi* (Stannard, 1970) **comb. n.**  
*Stephanothrips quadratus* (Okajima & Urushihara, 1995) **comb. n.**  
*Stephanothrips ryukyuensis* (Okajima, 1994) **comb. n.**

## References

- Ananthakrishnan, T.N. (1964) Thysanopterologica Indica II. *Entomologisk Tidskrift*, 85, 218–235.
- Ananthakrishnan, T.N. (1966) Thysanopterologica Indica—IV. *Bulletin of Entomology, India*, 7, 1–12.
- Ananthakrishnan, T.N. (1968) Studies on new and little known Indian Thysanoptera. *Oriental Insects*, 1, 113–138.  
<https://doi.org/10.1080/00305316.1967.10433856>
- Bagnall, R.S. (1909) On *Urothrips paradoxus*, a new type of Thysanopterous insects. *Annales Historico-Naturales Musei Nationalis Hungarici*, 7, 125–136.
- Bhatti, J.S. (2002) Identification of the urothripid *Baenothrips asper* (Bournier, 1963) (Tubulifera: Urothripidae). *Oriental Insects*, 36, 1–28.  
<https://doi.org/10.1080/00305316.2002.10417316>
- Bianchi, F.A. (1946) *Conocephalothrips tricolor*, a new urothripid from Hawaii. *Proceedings of the Hawaiian entomological Society*, 12, 499–502.
- Bournier, A. (1963) Thysanoptères de l'Angola II. *Publicações Culturais da Companhia de Diamantes de Angola*, 63, 73–86.
- Buckman, R.S., Mound, L.A. & Whiting, M.F. (2013) Phylogeny of thrips (Insecta: Thysanoptera) based on five molecular loci. *Systematic Entomology*, 38, 123–133.  
<https://doi.org/10.1111/j.1365-3113.2012.00650.x>
- Buffa, P. (1909) Contribuzione alla conoscenza dei Tisanotteri (due nuovi generi di Tubuliferi). *Bolletino Zoologia agraria Portici*, 3, 193–199.
- Crawford, J.C. (1948) A new genus of Urothripidae from Guatemala. *Proceedings of the Entomological Society of Washington*, 50, 39–40.
- Hood, J.D. (1925) New neotropical Thysanoptera collected by C.B. Williams. *Psyche*, 32, 48–69.  
<https://doi.org/10.1155/1925/38498>
- Hood, J.D. (1930) Two Urothripidae (Thysanoptera) from Florida, with keys to the known genera and the North American species. *Bulletin of the Brooklyn Entomological Society*, 24, 314–322.
- Minaei, K. & Mound, L.A. (2021) Character-state evaluation when discriminating Thysanoptera taxa (Insecta). *Zootaxa*, 5061 (2), 377–382.  
<https://doi.org/10.11646/zootaxa.5061.2.10>
- Mound, L.A. (1970) Thysanoptera from the Solomon Islands. *Bulletin of the British Museum (Natural History). Entomology*, 24, 83–126.  
<https://doi.org/10.5962/bhl.part.1519>
- Mound, L.A. (1972) Species complexes and the generic classification of leaf-litter thrips of the Tribe Urothripini (Phlaeothripidae). *Australian Journal of Zoology*, 20, 83–103.  
<https://doi.org/10.1071/ZO9720083>
- Mound, L.A. (1977) Species diversity and the systematics of some New World leaf-litter Thysanoptera (Phlaeothripinae; Glyptothripini). *Systematic Entomology*, 2, 225–244.  
<https://doi.org/10.1111/j.1365-3113.1977.tb00371.x>
- Mound, L.A. (1983) Natural and disrupted patterns of geographical distribution in Thysanoptera (Insecta). *Journal of Biogeography*, 10, 119–133.  
<https://doi.org/10.2307/2844623>
- Mound, L.A. & Wells, A. (2023) Endemism among Lord Howe Island Thysanoptera, with new species of *Baenothrips* (Phlaeothripidae) and *Scirtothrips* (Thripidae). *Zootaxa*, 5228 (1), 81–91.  
<https://doi.org/10.11646/zootaxa.5228.1.5>
- Okajima, S. (1987) Some Thysanoptera from the East Kalimantan, Borneo, with descriptions of a new genus and five new species. *Transactions of the Shikoku Entomological Society*, 18, 289–299.
- Okajima, S. (1989) Five new species of the genus *Stephanothrips* (Thysanoptera, Phlaeothripidae) from Southeast Asia, with a key to the East Asian species. *Japanese Journal of Entomology*, 57, 25–36.
- Okajima, S. & Urushihara, H. (1995a) Descriptions of four new urothripine species (Thysanoptera, Phlaeothripidae) from south east Asia. *Japanese Journal of Systematic Entomology*, 1, 27–34.
- Okajima, S. & Urushihara, H. (1995b) Studies on some *Stephanothrips* species (Thysanoptera: Phlaeothripidae) from Southeast Asia. *Japanese Journal of Systematic Entomology*, 1, 227–233.

- Priesner, H. (1931) Ein neues Genus aus der Familie Urothripidae. *Konowia*, 10, 93–95.
- Stannard, L.J. (1952) A new Australian Phlaeothripidae (Thysanoptera: Tubulifera). *Proceedings of the Biological Society of Washington*, 66, 127–130.
- Stannard, L.J. (1957) The phylogeny and classification of the North American genera of the sub-order Tubulifera (Thysanoptera). *Illinois Biological Monographs*, 25, 1–200.  
<https://doi.org/10.5962/bhl.title.50287>
- Stannard, L.J. (1970) New genera and species of Urothripini (Thysanoptera: Phlaeothripidae). *Proceedings of the Royal Entomological Society of London B*, 39, 114–124.  
<https://doi.org/10.1111/j.1365-3113.1970.tb00264.x>
- Tong XL & Zhao C (2017) Review of fungus-feeding urothripine species from China, with descriptions of two new species (Thysanoptera: Phlaeothripidae). *Zootaxa*, 4237 (2), 307–320.  
<https://doi.org/10.11646/zootaxa.4237.2.5>
- Trybom, F. (1912) Physapoden aus Natal und dem Zululande. *Arkiv för Zoologi*, 7 (33), 1–52.  
<https://doi.org/10.5962/bhl.part.17454>
- Ulitzka, M.R. & Mound, L.A. (2014) New generic synonyms in the Palaeotropical genus *Urothrips* (Thysanoptera: Phlaeothripinae) with one new species from Seychelles. *Zootaxa*, 3755 (6), 595–600.  
<https://doi.org/10.11646/zootaxa.3755.6.6>