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Systematic significance of antennal segmentation and sense cones in Thripidae (Thysanoptera: Terebrantia)

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Abstract

Variation is discussed concerning the number of antennal segments in adults, and the number of their sense cones, among 182 of the 289 genera of Thripidae. Brief comments are also made concerning antennal structure and sensoria among the other seven terebrantian families. The plesiotypic condition for Thysanoptera is 9-segmented antennae, but fusion between various segments leads to a reduction in number to as few as five segments, and such fusion occurs in unrelated species. In Thripidae, antennal segment III never bears more than one sense cone, but the distribution of sense cones on segments IV–VIII varies and is tabulated. On antennal segment IV, species in nearly all Panchaetothripinae genera and more than half of Thripinae genera have two sense cones, but genera of Dendrothripinae and Sericothripinae bear only one on this segment. The differing patterns of segmental fusion that occur in Thripidae are discussed in association with the number of sense cones on VI–VIII; species with 7, 8 or 9 segmented antennae almost always lack a sense cone on the terminal segment. It is concluded that the number of antennal segments is subject to irregular homoplasy, and is thus sometimes an unreliable indicator of relationships.

Key words: sensilla, plesiomorphy, segment sub-division/fusion, antennal sense cones

Introduction

In the insect Order Thysanoptera, the number of antennal segments in adults, and the form of their major antennal sensoria, are of fundamental importance in taxon recognition and classification at all levels, from family to species (Mound *et al*. 1980). Emergent sense cones on antennal segments III and IV occur only in the members of three families, whereas in the other six families the sensoria on these two segments are linear and non-emergent, and this latter condition is generally accepted as the plesiomorphic condition. Concerning the number of antennal segments, nine appears to be plesiotypic, because it occurs in almost all of the species that retain other plesiomorphic character states (Mound *et al*. 1980). Moreover, it also occurs in the oldest available fossils, although the number in Triassothripidae, a basal and fossil clade among the Thysanoptera, is stated to be "at least six segments" (Grimaldi *et al.* 2004). Antennae of this form are typical of 27 of the 47 Terebrantia genera known only from fossils (Appendix 1). However, amongst the 20 fossil genera of Thripidae, 9-segmented antennae are reported in a further seven genera, of which four are Dendrothripinae and three are attributed to Thripinae. The number of segments is thus considered to be reduced in the more recent and highly derived taxa. As a result, having seven or eight segments with emergent sense cones on III and IV, is the most common condition found amongst present-day Thysanoptera species.

There are problems with the concept of antennal segment fusion and reduction in number of segments. For example, segment VIII might fuse with IX, or segment VIII might fuse with VII. Both of these would produce an 8-segmented condition from a 9-segmented condition, and the presence of 8-segmented antennae would thus not necessarily represent a shared apomorphy. Moreover, a few taxa with 9-segmented antennae appear to be highly derived, based on other morphological characters. The condition in these species seems more likely to be reversion

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from an 8-segmented condition, resulting from sub-division of one or other unspecified segments, rather than a retained plesiomorphy. The objective of the study reported here was to try to elucidate homologies between the antennal segments of different taxa through a comparative study of their major sensoria. Emphasis here is on the variation exhibited among members of the large and widespread family Thripidae.

Antennal sensory structures of Thysanoptera species have generally been referred to by taxonomists as "sensoria", particularly when these structures are non-emergent (Marullo 1998). However, when clearly protruding from a segment they are referred to as "trichomes" (Mound *et al*. 1980), or more frequently as "sense cones". The latter term was mentioned originally by Hind (1902), but antennae bear more than one kind of sensory structures. Slifer & Sekhon (1974) recognised the major sense cones as thin-walled chemoreceptors, that is *sensilla basiconica*, in contrast to thick-walled *sensilla chaetica* and other sensoria that occur on thrips antennae (De Facci *et al*. 2011). The *sensilla basiconica* are presumably significant in behaviour, but they exhibit a diversity of shapes, sizes and distributions among Thysanoptera species. In the absence of detailed electron microscopy studies, the large *sensilla basiconica* typical of antennal segments III and IV are here considered homologous with the smaller sense cones that occur on several of the more distal segments.

Two sub-orders are recognised in the Thysanoptera, and the antennal sense cones are always simple in the members of the larger of these two groups—the Tubulifera with its single extant family of over 3000 species, the Phlaeothripidae. In this family, the plesiotypic number of sense cones on antennal segments III and IV is probably one on III and three on IV (Mound *et al.* 1980). However, the number of sense cones on these two segments is highly variable among the family members. On segment III it ranges from 0 in species of *Lissothrips* (Mound & Marullo 1996) to 20 in some species of *Ecacanthothrips* (Palmer & Mound 1978), but with three on III and four on IV being the most frequent condition. Moreover, members of Tubulifera usually have eight antennal segments; reduction in this number is rare, down to as few as four segments. However, a single species placed in the family Rohrthripidae, a fossil from Cretaceous Burmese Amber, has nine segments (Ulitzka 2018). In contrast, the sub-order Terebrantia comprises about 2000 species in eight extant families, and the number of segments, and the sensoria on segments III and IV, vary greatly between the members of these families. Before examining in detail the range of antennal variation in the Thripidae, we first summarise the diversity found among the smaller extant families of Terebrantia.

Antennal variation among families of Thysanoptera-Terebrantia

All of the observations recorded here are based on specimens examined at the Australian National Insect Collection, Canberra. The number of antennal segments was considered in the phylogenetic analysis of relationships amongst Thysanoptera families (Mound *et al*. 1980). In that analysis it was concluded that 9-segmented antennae were plesiotypic for the Thysanoptera, and occurred in all of the least derived families. This conclusion is further supported by the phylogenetic analysis of Buckman *et al*. (2013) that was based on molecular data. Among the eight families of Terebrantia, the Uzelothripidae is known from a single living species. The structure of the 7-segmented antennae (Fig. 25) is unlike that of any other thysanopteran, and relationships of this species to the other Thysanoptera remain obscure (Mound *et al*. 1980). Segments IV to VII form a whip-like structure, segment III bears a unique circular sensorium, and IV–V each have a simple sense cone (Fig. 25). In the remaining seven families of Terebrantia, 9-segmented antennae occur in at least some species of six of them. Melanthripidae and Merothripidae retain several structural character states in a plesiomorphic condition, including the presence in females of the remnants of abdominal sternite VIII (Mound *et al*. 1980). Species in these families have 9-segmented antennae (although only 8 in *Merothrips* species), and segments III and IV each have a single small, transverse sensorium (Figs 24, 28). The family Fauriellidae comprises four genera with a total of five species. These all have 9-segmented antennae (Fig. 27) (eight in one species), and the sensoria on segments III and IV are similar to those of the Merothripidae. In the Neotropical and Nearctic family Heterothripidae antennae are 9-segmented (Fig. 22) with the sensoria on segments III and IV similar to some species of Melanthripidae in having porous, circum-polar sensorial bands. In contrast, species in the large and widespread family Aeolothripidae have 9-segmented antennae (Fig. 23), but the sensoria on III and IV are usually linear, often elongate along these segments. Almost all of the species in this family have only one sensorium on each of these two segments, but about five species are known to have two sensoria on each. Finally, the Stenurothripidae and Thripidae share the

presence of emergent sense cones on segments III and IV. The family Stenurothripidae comprises six living species in three genera, together with several fossil taxa, and all of these have 9-segmented antennae (Fig. 26) with broadly conical sense cones. In contrast the Thripidae is a group of nearly 2100 species in almost 300 genera, in all of which the sense cones are slender, and in which the number of segments is eight or less in more than 2000 species. This study is focused on the antennal sense cones found among members of the family Thripidae. These structures are always simple on segments V–VIII, but on segments III and IV they may be either simple or forked. However, in all Thripidae species only a single sense cone is present on segment III, and this segment is therefore not considered further. Here we discuss the distribution of sense cones on segments IV–VIII for each of the four recognised subfamilies of family Thripidae (ThripsWiki 2018): Dendrothripinae, Panchaetothripinae, Sericothripinae and Thripinae.

Sense cones among Dendrothripinae

The subfamily Dendrothripinae comprises about 105 species in 12 genera (ThripsWiki 2018), and representative species of nine genera are included in this study (Table 1). In this subfamily, the antennae of more than 50% of species are 8-segmented, of nearly 30% of species are 9-segmented, and in only a few species are 7-segmented. Throughout this subfamily, antennal segment IV has one sense cone, and segment V two (except the two species in *Edissa* that have only one on V). In species with 8-segmented antennae (Fig. 1), segment VIII lacks sense cone. Most species have three sense cones on VI, and one or none on VII, but species of both *Halmathrips* and *Pseudodendrothrips* that have 8-segmented antennae have two sense cones on VI and two or one on VII. In species of these two genera that have 9-segmented antennae (Fig. 7), segments VI and VII have two and one sense cones respectively, VIII has one or none, IX has none. This configuration suggests that in these species with nine antennal segments, the seventh morphological segment has divided to produce the apparent VII and VIII (Figs 7, 32). However, other species in Dendrothripinae with 9-segmented antennae (Figs 5, 6) have two sense cones on VI and one on VII and VIII but none on IX, or three on VI and one on VIII but none on VII and IX (Figs 30, 31). This arrangement suggests that segment VI has subdivided in these species (Figs 5, 6, 30, 31), and emphasises the lack of evidence that 9-segmented antennae might be plesiomorphic within this sub-family. In the two species of *Edissa* (Fig. 3), also eight species in *Dendrothrips* with 7-segmented antennae (Fig. 4), VII lacks sense cones, although one sense cone is present on VII in most species of *Leucothrips* (Fig. 2). This implies that the terminal segment (the seventh) is not homologous in species of these genera; fusion in *Leucothrips* has occurred between the two terminal segments (Figs 2, 33), but in *Dendrothrips* and *Edissa* fusion has occurred between two of the sub-terminal segments (Figs 3, 4, 34).

TABLE 1. Sense cones distribution in genera of Thripidae-Dendrothripinae

	Antennal segments	IV	V	VI	VII	VIII	IX	Total number
Asprothrips	8	1	2	3	1/0	0		6/7
Dendrothrips	7	1	2	4	0			7
Dendrothrips	8	1	2	3	1	0		7
Dendrothrips	9	1	2	2	1	1	0	7
Edissa	7	1	1	3	0			5
Ensiferothrips	9	1	2	3	0	1	0	7
Filicopsothrips	9	1	2	2	1	1	0	7
Halmathrips	8	1	2	2	2	0		7
Halmathrips	9	1	2	2	1	1	0	7
Iranodendrothrips	8	1	2	3	1	0		7
Leucothrips	7	1	2	2	1			6
Pseudodendrothrips	8	1	2	2	1	0		6
Pseudodendrothrips	9	1	2	2	1	0	0	6

Sense cones among Panchaetothripinae

The subfamily Panchaetothripinae comprises about 140 species in 40 genera (ThripsWiki 2018), and species of 26 genera have been examined for this study (Table 2). Antennae are usually 8-segmented, but segmental fusion is evident in five of the genera studied. The six species in the three genera *Phibalothrips*, *Moundothrips* and *Parthenothrips* all have 7-segmented antennae, but among the 12 species of *Astrothrips* the number of segments varies from eight to six, and among the four species of *Bhattithrips* the range is from eight to five segments. In species of seven genera that were placed by Wilson (1975) in the Tribe Panchaetothripini, antennal segment IV bears a single sense cone: *Arachisothrips*, *Australothrips*, *Euidothrips*, *Moundothrips*, *Neoheliothrips*, *Phibalothrips*, and *Sigmothrips*. However, in members of the remaining 19 of the 26 genera examined antennal segment IV bears two sense cones (Figs 9, 10, 12), and these genera represent all three of the Tribes recognised by Wilson. Reduction in the number of antennal segments among the species of *Bhattithrips* results in *B. frontalis* with 5-segmented antennae having five sense cones on segment V, but *B. borealis* with 6-segmented antennae (Fig. 11) having four on segment V but none on VI. Most Panchaetothripinae species have two sense cones on segment VI and one on VII (Fig. 12), but *Euidothrips* is remarkable with three sense cones on VI, and the species of *Astrothrips* with 6-segmented antennae also have three on VI. The species of *Moundothrips*, *Parthenothrips* and *Phibalothrips* having 7-segmented antennae bear three sense cones on VI but none on VII; this can be interpreted as indicating that morphological segments VI and VII have fused leaving VIII as the visible seventh segment (Figs 13, 34). However, the 7-segmented antennae of *Astrothrips tumiceps* have two sense cones on VI and one on VII, suggesting that morphological segment VIII has fused with VII (Figs 8, 33). In 8-segmented species, the terminal segment apparently never bears a sense cone. We deduce from these complexities that various patterns of antennal segment fusion have occurred amongst Panchaetothripinae species.

Sense cones among Sericothripinae

The subfamily Sericothripinae comprises more than 160 species in 3 genera (ThripsWiki 2018), although this generic classification probably does not reflect real phylogenetic relationships (Lima & Mound 2016). Antennae are nearly always 8-segmented, although several species in each of *Hydatothrips* and *Neohydatothrips* have only seven segments (Table 3). Antennal segment IV always bears one sense cone, but the number on V is variable with two sense cones being the most common. In *Neohyatothrips* and *Hydatothrips*, segment VI usually has three sense cones of which one has an exceptionally long narrow base (Fig. 14). Moreover, one of the sense cones on segment V commonly has a relatively long narrow base, and this also occurs in some *Sericothrips* species. All species in this sub-family have a single sense cone on VII, even when the antenna is 7-segmented and VIII is presumably fused with segment VII (Figs 15, 33).

Sense cones among Thripinae

The Thripinae, with 234 genera and slightly more than 1700 species (ThripsWiki 2018), is the largest subfamily of Thripidae, and representative species of 144 genera were included in this study. The species have a wide range of feeding habits, but are mainly either flower- or leaf-feeding, with a few predatory on other small arthropods. The distribution of antennal sense cones among most genera of Thripinae is indicated in Table 3. To facilitate discussion, various genus-group within the Thripinae are mentioned below; these were proposed by Mound and Palmer (1981) and also by Masumoto and Okajima (2017; 2018).

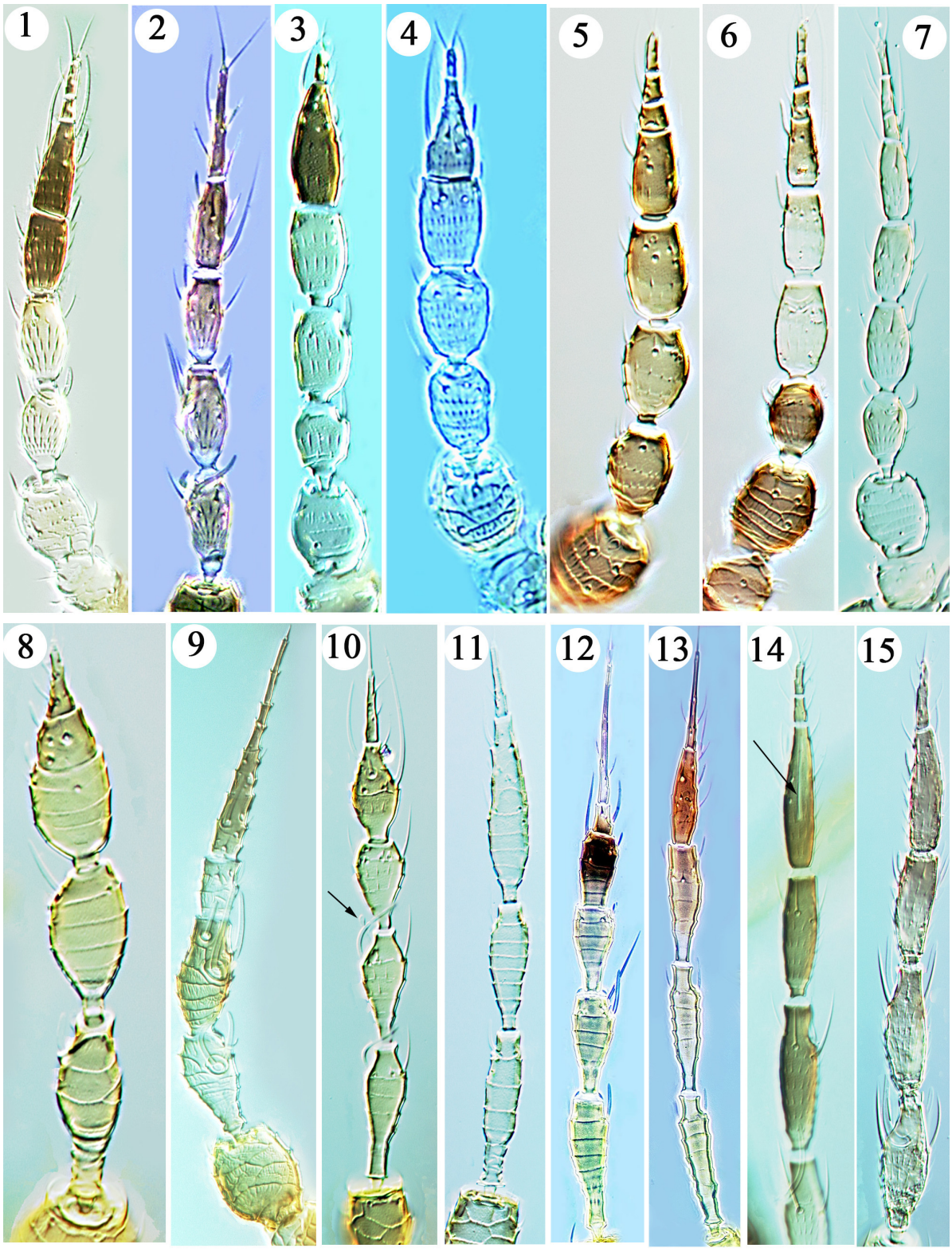
Antennal segment IV of Thripinae species usually bears two sense cones, but one is large and either simple or forked whilst the second is very small and simple. Similarly, segment V bears two sense cones, both simple and with one much smaller than the other. However, representatives were available for this study of nine of the eleven genera of the *Scirtothrips* genus-group (Ng & Mound 2015), and nearly each of these was found to have only one sense cone on both IV and V: *Anascirtothrips*, *Biltothrips*, *Cercyothrips*, *Drepanothrips*, *Kenyattathrips* (two on segment V), *Parascirtothrips*, *Scirtidothrips* (two on segment V), *Scirtothrips* (some species have two on segment V), *Siamothrips*. Similarly, species of *Amalothrips*, *Exothrips*, *Parexothrips*, and *Rhamphothrips* that comprise the

Rhamphothrips genus-group also have only one sense cone on IV and V. Some genera of *Anaphothrips* genus-group, *Ameranathrips*, *Aptinothrips*, *Aurantothrips*, *Belothrips*, *Desertathrips*, *Eremiothrips*, *Pandorathrips*, *Paroxythrips*, *Pseudothrips* and *Tameothrips*, also share the reduced number of sense cones on segment IV, but the number on V is variable.

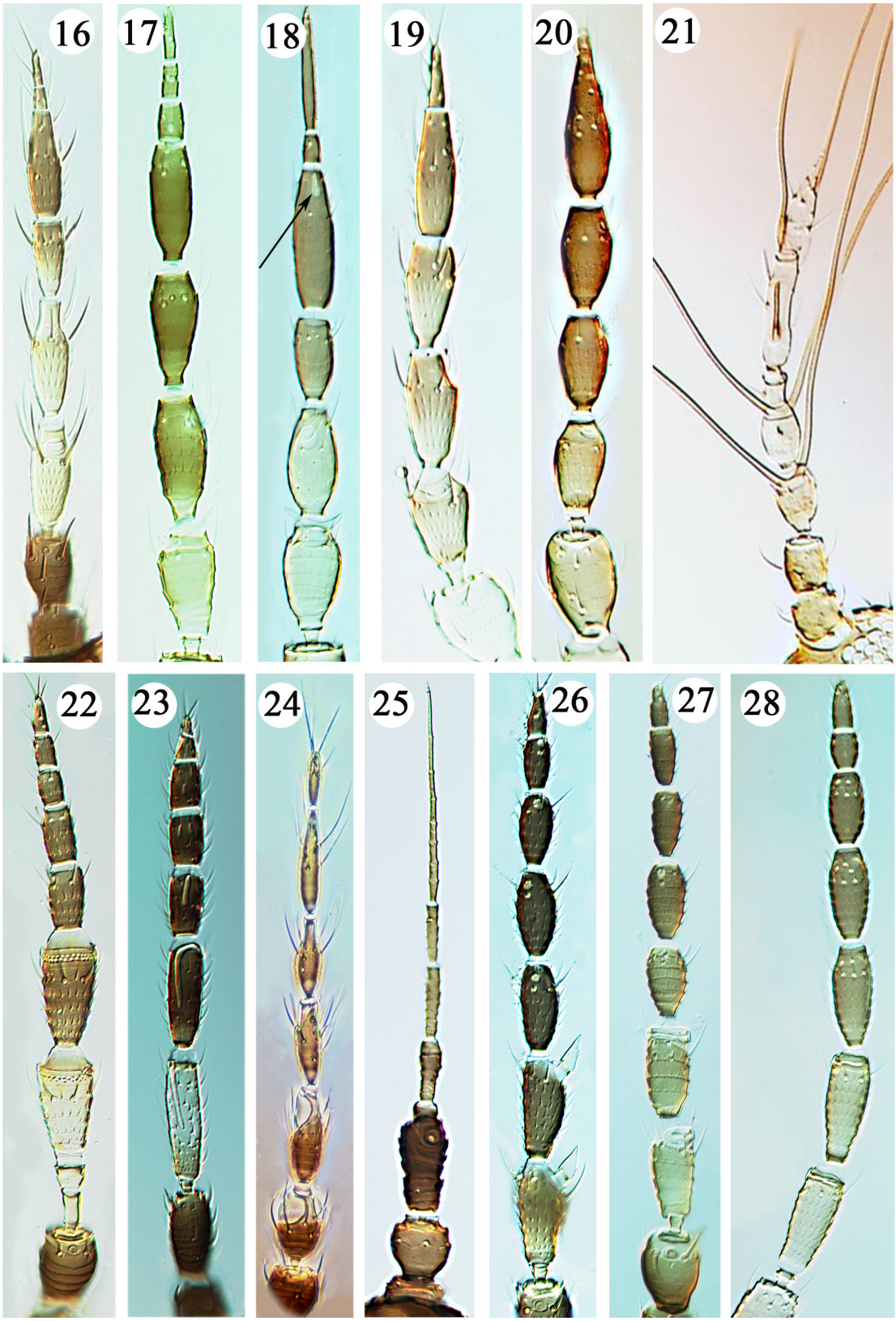
Thripinae genera that are usually considered to be the more highly derived comprise species that have two sense cones on both of antennal segments IV and V. These genera include the *Megalurothrips* genus-group (*Ceratothripoides*, *Ceratothrips*, *Megalurothrips* (Fig. 16), *Odontothrips*, *Odontothripiella* and *Projectothrips*), as well as some more distantly related genera: *Bregmatothrips*, *Craspedothrips* and *Sorghothrips*. Moreover, a similar condition is found in *Thrips* genus-group (*Baliothrips*, *Bolacothrips*, *Ernothrips*, *Fulmekiola* (one on IV), *Larothrips*, *Microcephalothrips*, *Sphaeropothrips*, *Stenchaetothrips*, *Stenothrips* and *Thrips*), and most of *Frankliniella* genus-group (*Frankliniella*, *Iridothrips*, *Kakothrips*, *Parabaliothrips*, *Pseudanaphothrips* and *Sitothrips*). Interestingly, *Filipinothrips* that is closely related to *Craspedothrips* (Tyagi *et al*. 2008) also has two sense cones on segment V, while species of *Indusiothrips* have none on this segment.

TABLE 2. Sense cones distribution in genera of Thripidae-Panchaetothripinae

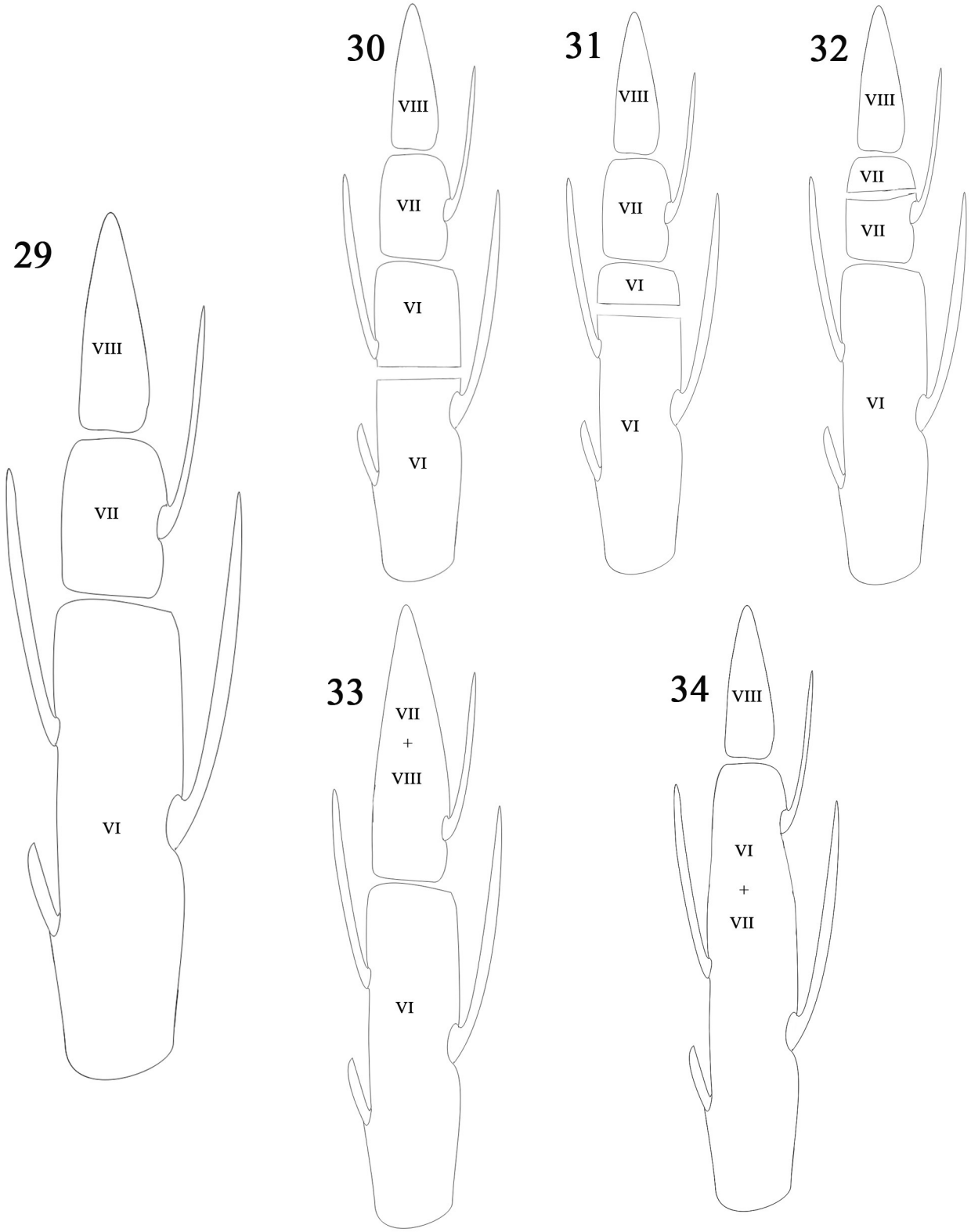
	Antennal segments	IV	V	VI	VII	VIII	Total number
Anisopilothrips	8	2	2	2	1	0	7
Aoratothrips	8	2	1	2	1	0	6
Arachisothrips	8	1	1	2	1	0	5
Araliacothrips	8	2	1	2	1	0	6
Astrothrips	6	2	1/2	3			6/7
Astrothrips	7	2	1/2	2	1		6/7
Australothrips	8	1	1	2	1	0	5
Bhattithrips	5	2	5				7
Bhattithrips	6	2	4	0			6
Bhattithrips	8	2	2	2	1	0	7
Caliothrips	8	2	1	2	1	0	6
Copidothrips	8	2	1	2	1	0	6
Dinurothrips	8	2	1/2	2	1	0	6/7
Elixothrips	8	2	1	2	1	0	6
Euidothrips	8	1	2	3	1	0	7
Helionothrips	8	2	1	2	1	0	6
Heliothrips	8	2	1	2	1	0	6
Hercinothrips	8	2	2	2	1	0	7
Monilothrips	8	2	1	2	1	0	6
Moundothrips	7	1	1	3	0		5
Neoheliothrips	8	1	1	2	1	0	5
Panchaetothrips	8	2	1/2	2	1	0	6/7
Parthenothrips	7	2	2	3	0		7
Phibalothrips	7	1	1	3	0		5
Retithrips	8	2	1	2	1	0	6
Rhipiphorothrips	8	2	1/2	2	1	0	6/7
Selenothrips	8	2	2	2	1	0	7
Sigmothrips	8	1	1	2	1	0	5
Zaniothrips	8	2	1	2	1	0	6



FIGURES 1–15. Antennal segments of Thripidae. Dendrothipinae 1–7: **(1)** *Asprothrips seminigricornis* segments I–VIII; **(2)** *Leucothrips nigripennis* segments II–VII; **(3)** *Edissa steinerae* segments I–VII; **(4)** *Dendrothrips glynn* segments I–VII; **(5)** *D. victoriae* segments II–IX; **(6)** *D. julatteni* segments I–IX; **(7)** *Pseudodendrothrips mori* segments I–IX. Panchaetothripinae 8–13: **(8)** *Astrothrips tumiceps* segments II–VII; **(9)** *Retithrips javanicus* segments II–VIII; **(10)** *Elixothrips brevisetis* segments II–VIII, arrow indicates extra sense cone with enlarged apex; **(11)** *Bhattithrips borealis* segments II–VI; **(12)** *Heliothrips haemorrhoidalis* segments III–VIII; **(13)** *Parthenothrips dracaenae* segments III–VII. Sericothripinae 14–15: **(14)** *Hydatothrips heteraureus* segments III–VIII; arrow indicates narrow base of sense cone; **(15)** *Neohydatothrips plynopygus* segments III–VII.



FIGURES 16–28. FIGURES 16–21. Antennal segments of Thripinae. **(16)** *Megalurothrips typicus* segments I–VIII; **(17)** *Anaphothrips occidentalis* segments III–IX; **(18)** *Projectothrips beverlyae* segments II–VIII, arrow indicates narrow base of sense cone; **(19)** *Anascirtothrips arorai* segments II–VII; **(20)** *Drepanothrips reuteri* segments II–VI; **(21)** *Aroidothrips longistylus* male antennal segments I–VI. **FIGURES 22–28.** Antennae. **(22)** *Heterothrips prosopidis* segments II–IX; **(23)** *Desmothrips uniguttus* segments I–IX; **(24)** *Erotidothrips mirabilis* segments II–IX; **(25)** *Uzelothrips scabrosus* segments I–VII; **(26)** *Oligothrips oreios* segments II–IX; **(27)** *Fauriella natalensis* segments II–IX; **(28)** *Dorythrips wallacei* segments II–IX.



FIGURES 29–34. Schematic of antennal segments division and fusion in Thripidae. **(29)** Antennal segments VI–VIII; **(30)** antennal segment VI sub-divided; **(31)** antennal segment VI sub-divided; **(32)** antennal segment VII sub-divided; **(33)** antennal segments VII and VIII fused; **(34)** antennal segments VI and VII fused.

TABLE 3. Sense cones distribution in genera of Thripinae and Sericothripinae
(* three unavailable species of *Frankliniella* are recorded as having 7-segmented antennae)

	Antennal segments	IV	V	VI	VII	VIII	IX	Total number
Adelphithrips	8	2	2	3	1	0		8
Alathrips	8	1	2	3	1	0		7
Aliceathrips	8	2	2	3	1	0		8
Amalothrips	8	1	1	2	0	0		4
Ameranathrips	8	1	2	3	1	0		7
Amomothrips	8	2	2	3	1	0		8
Anaphothrips	8	2	2	3	1	0		8
Anaphothrips	9	2	2	2	1	1	0	8
Anascirtothrips	7	1	1	2	1			5
Aneristothrips	8	1	2	3	1	0		7
Apterothrips	8	2	2	3	1	0		8
Apterothrips	9	2	2	2	1	1	0	8
Aptinothrips	6	1	1	3				5
Aptinothrips	8	1	1	3	0	0		5
Aroidothrips	8	1	2	3	0	0		6
Arorathrips	8	2	2	3	1	0		8
Arpediothrips	8	2	2	2	?	0		?
Asphodelothrips	8	2	2	3	1	0		8
Aurantothrips	8	1	2	3	1	0		7
Ayyaria	8	1	2	3	1	0		7
Baileyothrips	8	2	2	3	1	0		8
Baliothrips	7	2	2	3	1			8
Bathrips	8	1	2	3	0	0		6
Belothrips	8	1	1	2	1	0		5
Biltothrips	8	1	1	2	1	0		5
Bolacothrips	7	2	2	3	1			8
Bradinothrips	8	2	1	2	1	0		6
Bravothrips	8	2	2	3	1	0		8
Bregmatothrips	7	2	2	3	1			8
Bregmatothrips	8	2	2	3	1	0		8
Brooksithrips	7	2	2	2	1			7
Ceratothripoides	8	2	2	3	1	0		8
Ceratothrips	8	2	2	3	1	0		8
Cercyothrips	8	1	1	2	?	0		?
Chaetanaphothrips	8	2	2	3	1	0		8
Chaetisothrips	8	2	2	3	1	0		8
Charassothrips	8	2	2	3	1	0		8
Chirothrips	8	2	2	3	1	0		8
Clypeothrips	8	2	2	3	1	0		8
Collembolothrips	8	2	2	3	1	0		8
Coremothrips	9	1	1	2	1	1	0	6

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TABLE 3. (Continued)

	Antennal segments	IV	V	VI	VII	VIII	IX	Total number
Corynothrips	9	1	1	2	1	0	0	5
Craspedothrips	8	2	2	3	1	0		8
Ctenothrips	8	2	2	3	1	0		8
Cyrilthrips	8	2	2	3	1	0		8
Danothrips	8	1	2	3	1	0		7
Dendrothripoides	8	1	2	3	1	0		7
Desertathrips	9	1	2	2	1	1	0	7
Diathrothrips	8	2	2	2	1	0		7
Dichromothrips	8	2	2	3	1	0		8
Dictyothrips	8	2	1	3	1	0		7
Dikrothrips	8	?	2	3	1	0		?
Drepanothrips	6	1	1	3				5
Echinothrips	8	2	2	3	1	0		8
Enneothrips	9	2	2	2	1	1	0	8
Eremiothrips	8	1	2	3	1	0		7
Eremiothrips	9	1	2	2	1	1	0	7
Exothrips	8	1	1	3	0	0		5
Ernothrips	7	2	2	2	1			7
Euphysothrips	8	2	2	3	1	0		8
Ficothrips	9	1	2	2	1	1	0	7
Filipinothrips	8	2	2	3	1	0		8
Florithrips	8	2	2	2	1	0		7
*Frankliniella**	8	2	2	3	1	0		8
Fulmekiola	7	1	2	3	1			7
Glaucothrips	8	2	2	3	1	0		8
Hengduanothrips	7	1	2	2	1			6
Hydatothrips	7	1	2	3	1			7
Hydatothrips	8	1	1/2	3	1	0		6/7
Indusiothrips	8	1	0	3	0	0		4
Iridothrips	8	2	2	3	1	0		8
Isunidothrips	8	2	2	3	0	0		7
Kakothrips	8	2	2	3	1	0		8
Karphothrips	8	1	2	2	1	0		6
Kenyattathrips	7	1	2	3	1			7
Kranzithrips	8	2	2	3	1	0		8
Kurtomathrips	8	1	1	3	1	0		6
Larothrips	7	2	2	?	1			?
Lefroyothrips	8	2	2	3	1	0		8
Limothrips	8	?	2	3	1	0		?
Lomatothrips	7	1	2	3	1			7
Masamithrips	8	1	1	3	1	0		6
Megalurothrips	8	2	2	3	1	0		8

.....continued on the next page

TABLE 3. (Continued)

	Antennal segments	IV	V	VI	VII	VIII	IX	Total number
Microcephalothrips	7	2	2	3	1			8
Monothrips	8	2	2	3	1	0		8
Mycterothrips	8	2	2	3	1	0		8
Neocorynothrips	8	2	2	3	1	0		8
Neohydatothrips	7	1	2	3	1			7
Neohydatothrips	8	1	1/2	3	1	0		6/7
Nexothrips	8	2	2	3	1	0		8
Octothrips	8	2	1	3	?	0		?
Odontothripiella	8	2	2	3	1	0		8
Odontothrips	8	2	2	3	1	0		8
Okajimaella	8	2	2	3	1	0		8
Organothrips	8	2	2	2	1	0		7
Oxythrips	8	2	2	3	1	0		8
Ozanaphothrips	8	2	2	3	1	0		8
Paithrips	8	2	2	3	1	0		8
Palmiothrips	9	2	2	2	1	1	0	8
Pandanothrips	8	1	2	3	1	0		7
Pandorathrips	8	1	2	3	1	0		7
Parabaliothrips	8	2	2	3	1	0		8
Paraleucothrips	8	1	1	3	1	0		6
Parascirtothrips	7	1	1	3	1			6
Parascolothrips	7	2	1	2	1			6
Parexothrips	8	1	1	3	0	0		5
Paroxythrips	8	1	1	3	1	0		6
Pezothrips	8	2	2	3	1	0		8
Physemothrips	8	2	2	3	1	0		8
Platythrips	7	2	2	3	1			8
Plesiothrips	7	2	2	3	1			8
Priesneriola	6	2	2	3				7
Prionotothrips	8	1	1	3	1	0		6
Projectothrips	8	2	2	3	1	0		8
Proscirtothrips	9	2	2	2	1	1	0	8
Prosopoanaphothrips	8	1	1	3	1	0		6
Prosopothrips	8	1	1	3	1	0		6
Psectrothrips	9	2	2	2	1	1	0	8
Pseudanaphothrips	8	2	2	3	1	0		8
Pseudothrips	8	1	2	3	1	0		7
Pseudothrips	9	1	2	2	1	1	0	7
Psilothrips	8	1	1	2	1	0		5
Psydrothrips	9	2	2	2	1	1	0	8
Pteridothrips	8	2	2	3	0	0		7
Retanathrips	8	2	2	3	1	0		8

.....continued on the next page

TABLE 3. (Continued)

	Antennal segments	IV	V	VI	VII	VIII	IX	Total number
Rhamphiskothrips	8	1	?	?	?	?		?
Rhamphothrips	8	1	1	3	1	0		6
Rhaphidothrips	8	1	2	3	1	0		7
Rubiothrips	8	2	2	3	1	0		8
Salpingothrips	8	2	1	3	1	0		7
Sciothrips	8	2	2	3	1	0		8
Scirtidothrips	8	1	2	3	1	0		7
Scirtothrips	7	1	1	3	1			6
Scirtothrips	8	1	1/2	2/3	1	0		5–7
Scolothrips	8	1	1	3	1	0		6
Sericothrips	8	1	2	3	1			7
Siamothrips	8	1	1	3	1	0		6
Simulothrips	8	2	2	3	1	0		8
Sitothrips	8	2	2	3	1	0		8
Sorghothrips	8	2	2	3	1	0		8
Sphaeropothrips	7	2	2	3	1			8
Stenchaetothrips	7	2	2	3	1			8
Stenothrips	7	2	2	3	1			8
Striathrips	8	2	2	3	1	0		8
Synaptothrips	8	2	2	3	1	0		8
Synaptothrips	9	2	2	2	1	1	0	8
Taeniothrips	8	2	2	3	1	0		8
Takethrips	8	2	2	3	1	0		8
Tameothrips	8	1	2	3	1	0		7
Tenothrips	8	2	2	3	1	0		8
Thrips	7	2	2	3	1			8
Thrips	8	2	2	3	1	0		8
Tmetothrips	8	2	2	3	1	0		8
Trichromothrips	8	2	1/2	3	1	0		7/8
Tsutsumiothrips	7	1	2	3	1			7
Tusothrips	8	2	2	3	0	0		7
Yaobinthrips	8	2	2	3	1	0		8
Yaoshinothrips	8	2	2	3	1	0		8

Some species in several genera of Thripinae have 9-segmented antennae, and these all have two sense cones on segment VI, and one on each of segments VII and VIII, but none on IX (Fig. 30) (*Anaphothrips*, *Apterothrips*, *Coremothrips*, *Corynothrips*, *Desertathrips*, *Enneothrips*, *Eremiothrips*, *Ficothrips*, *Palmiothrips*, *Proscirtothrips*, *Psectrothrips*, *Pseudothrips*, *Psydrothrips* and *Synaptothrips*). However, species of several other genera have 7-segmented antennae, and these always have one sense cone on segment VII, but two or three on segment VI (Fig. 33) (*Anascirtothrips*, *Baliothrips*, *Bolacothrips*, (some) *Bregmatothrips*, *Brooksithrips*, *Ernothrips*, *Fulmekiola*, *Hengduanothrips*, *Kenyattathrips*, *Larothrips*, *Lomatothrips*, *Microcephalothrips*, *Parascirtothrips*, *Parascolothrips*, *Platythrips*, (some) *Plesiothrips*, (some) *Scirtothrips*, *Sphaeropothrips*, *Stenchaetothrips,* *Stenothrips*, (some) *Thrips* and *Tsutsumiothrips*). Species in three genera (*Aptinothrips*, *Drepanothrips* and *Priesneriola*) have 6-segmented antennae, and their distal segment has three sense cones. The most common condition of the distal antennal segments amongst Thripinae is segment VI with three sense cones, VII with one

and VIII with none (Fig. 29). However, in a few genera with 8-segmented antennae (*Amalothrips*, *Arpediothrips*, *Belothrips*, *Biltothrips*, *Diarthrothrips*, *Florithrips*, *Karphothrips*, *Organothrips*, *Psilothrips* and (some) *Scirtothrips*) there are only two sense cones on segment VI. *Projectothrips* species have an unusually long segment VIII, but this bears no sense cones. Interestingly, one of the sense cones on segment VI sometimes has a relatively long base in *Projectothrips beverlyae* (Fig. 18) from Australia, although the only other available species, *P. bhattii*, lacks this unusual long base.

Discussion

The morphological evidence, and also the available molecular evidence (Buckman *et al*. 2013), indicate that the subfamilies Dendrothripinae, Panchaetothripinae and Sericothripinae are each monophyletic. However, there is little evidence concerning their relationships to the Thripinae, and this major subfamily is presumably paraphyletic with respect to these three groups. The aim of the present study was to produce evidence from a restricted set of characters, antennal segmentation and antennal sense cones, that might be helpful in examining phylogenetic relationships among these groups of thrips. The morphology and geography of species of the *Thrip*s genus-group and *Frankliniella* genus-group suggest that these two groups represent two of the most recently derived Thripinae (Mound 2002). Among these species the most common situation on segment IV is the presence of two sense cones, as in most genera of Panchaetothripinae. However, despite this shared condition it seems likely that two independent apomorphies are involved, because the second sense cone on IV in Panchaetothripinae is unusually large (Figs 9, 10, 12) whereas it is small in Thripinae. If this second sense cone is not a shared apomorphy between these two subfamilies, then the sense cone has evolved independently within each of these lineages. Members of subfamily Sericothripinae share one sense cone on segment IV with species of *Scirtothrip*s genus-group; this presumably supports the close relationships between these two groups (Mound & Morris 2007; Buckman *et al*. 2013; Lima & Mound 2016). However, species of *Scirtothrip*s genus-group are mainly leaf-feeding, a biological habit shared with the species of Dendrothripinae that also share the plesiomorphic condition of one sense cone on segment IV. There is a possible correlation between feeding habits and the number of sense cones on segment IV amongst Thripinae, with one sense cone found in species associated with leaves or grasses, and two in species found mainly in flowers.

Among Thripidae the number of sense cones on antennal segments V–VIII is less than in most members of other Terebrantia families, and this may be related to the ways in which antennae are used. For example, species of Aeolothripidae are commonly ant-like in behaviour (Mound & Reynaud 2005), and actively use their antennae to explore their surroundings. The larger number of sensoria on the distal segments may be related to this behaviour. In contrast, species of Thripinae with 9-segmented antennae commonly have two sense cones on segment VI, one on each of VII and VIII, and none on IX (Fig. 30). This distribution of sense cones is found in *Psydrothrips* from the Neotropics, *Palmiothrips* from the Mediterranean region, and several of the *Anaphothrips* species from Australia, and in all of these the distal segments are particularly distinct from each other. *Palmiothrips* was placed near *Dendrothrips* on molecular data by Buckman *et al*. (2013), but this is contrary to the morphological data that might be interpreted as placing this taxon as a species of *Anaphothrips* with long antennae. The series of *Anaphothrips* from Australia indicate very strongly that the 9-segmented condition has evolved within this genus, from a partial oblique division on segment VI to a complete division of this segment (Figs 30, 31) (e.g. *Anaphothrips occidentalis* (Fig. 17) and some *Anaphothrips* fossil species (Schliephake 1993). The sense cones on segments VI–IX in these species with 9-segmented antennae are fare fewer than on these segments in species of Aeolothripidae, Melanthripidae and Merothripidae, hence the *Anaphothrips* condition is not plesiomorphic. Palmer and Mound (1985), in considering the 9-segmented antennae of *Synaptothrips* species from South Africa, suggested that this might be a retained plesiomorphy, because these species share with species of Aeolothripidae, Melanthripidae and Merothripidae the posterior position on the metanotum of the median setal pair. However, that suggestion is not supported by evidence from the sense cones on segments VI–IX of *Synaptothrips* species; these have no obvious difference from other Thripinae species with nine antennal segments. Four fossil genera of Dendrothripinae all have 9-segmented antennae. For three of these genera there is not enough information, but in *Synnastothrips* the 9-segmented condition possibly developed by sub-division of antennal segment VI, considering the obscure division between VI and VII (Schliephake 1993). However, some Dendrothripinae species, as

discussed above, have apparently developed 9-segmented antennae through subdivision of segment VII (Figs 7, 32); the 9-segmented condition in these species therefore cannot be considered as plesiomorphic. From these studies the various states of 9-segmented antennae among Thripidae are not homologous, but represent two or more independent apomorphies (Figs 30, 31, 32).

The fusion of antennal segments also demonstrates a complex situation. In Panchaetothripinae, antennal segment VI commonly bears two sense cones, and segment VII has one sense cone, although related species with 7-segmented antennae have three on segment VI and none on VII. This result is possibly because segments VI and VII fuse into a compact unit (Figs 13, 34), as in some Dendrothripinae species (Figs 3, 4). However, species with 7-segmented antennae in Thripinae and Sericothripinae have three sense cones on segment VI, and they usually bear one on segment VII (Fig. 33). This suggests the antennal fusion has occurred between segments VII and VIII (Figs 15, 19, 33), as in a few genera of two other subfamilies such as *Leucothrips* (Fig. 2) and *Astrothrips* (Fig. 8). Therefore, among Thripidae 7-segmented antennae have different origins (Figs 33, 34). The condition of 6-segmented antennae in Thripidae seems to result most commonly through fusion of segments VI, VII and VIII (Fig. 20). However, in *Bhattithrips borealis* there are four sense cones on segment V and none on VI. In this species the 6-segmented condition has probably resulted from fusion of segments V, VI and VII (Fig. 11).

Species of *Aroidothrips*, *Filipinothrips* and some *Mycterothrips* exhibit extreme sexual dimorphism in their antennae, with males bearing numerous and prominent sensoria and sensory setae (Masumoto & Okajima 2006, Tyagi *et al.* 2008). Males of *Aroidothrips* have 6-segmented antennae (Fig. 21), with one prominent sense cone on segment IV, four on V and three on VI, whereas females have 8-segmented antennae, and the sense cones on segments IV–VIII are one, two, three, absent, and absent respectively. However, males of *Mycterothrips* have 8-segmented antennae, and the number of antennal sense cones does not differ from that found in females; this is true also of species of *Filipinothrips.* In their use in exploring the environment, the number of antennal segments and sense cones are presumably at times under intense selection pressure. Under such circumstances, singular autapomorphies can be expected to arise from time to time. In the single species of the Panchaetothripinae genus, *Elixothrips*, the second large sense cone on IV is unique in having an enlarged apex (Fig. 10), and on V the number of sense cones is one. In another Panchaetothripinae genus, *Euidothrips*, the sense cones on segment IV in males are unusually prominent. Without careful studies on thrips behaviour, whether in relation to host-plant detection or to mating habits (Mound 2009), the function of the differences in antennal structure will remain conjectural. However, the information presented here concerning antennal segmentation and sense cones will be useful in testing phylogenetic relationships among genera of Thripidae.

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APPENDIX 1. Thysanoptera-Terebrantia genera known only from fossils
*Indicates presence of 9-segmented antennae

MEROTHRIPIDAE
† *Jezzinothrips* *
† *Myanmarothrips* *
† *Praemerothrips* *

MELANTHRIPIDAE
† *Archankothrips* *
† *Eocranothrips* *
† *Gymnopollisthrips* *
† *Proboscisthrips* *

AEOLOTHRIPIDAE
† *Cretothrips* *
† *Fusithrips* *
† *Lithadothrips* *
† *Palaeothrips* *
† *Permothrips* *
† *Rhipidothripoides* *
† *Sinaeolothrips* *

HEMITHRIPIDAE
† *Hemithrips* *

HETEROTHRIPIDAE
† *Electrothrips* *
† *Eocephalothrips* *
† *Protothrips* *

STENUROTHRIPIDAE
† *Exitelothrips* *
† *Hispanothrips* *
† *Neocomothrips* *
† *Opadothrips* *
† *Progonothrips* *
† *Rhetinothrips* *
† *Scaphothrips* *
† *Scudderothrips* *
† *Stenurothrips* *

THRIPIDAE—DENDROTHRIPINAE
† *Apodendrothrips* *
† *Praedendrothrips* *
† *Schedodendrothrips* *
† *Synnastothrips* *

THRIPIDAE—PANCHAETOTHRIPINAE
† *Archaeothrips*
† *Coccothrips*
† *Hoffeinsithrips*

THRIPIDAE—THRIPINAE
† *Amorphothrips*
† *Balticothrips*
† *Calothrips*
† *Convexithrips*
† *Eochirothrips*
† *Incertothrips*
† *Lewisothrips*
† *Lipsanothrips*
† *Procerothrips*
† *Protanaphothrips* *
† *Saxonothrips*
† *Telothrips* *
† *Tethysthrips* *