





https://doi.org/10.11646/zootaxa.5190.3.1

http://zoobank.org/urn:lsid:zoobank.org:pub:26F27376-45AB-4F13-ADCB-705CB3EB6E77

Convoluted maxillary stylets among Australian Thysanoptera Phlaeothripinae associated mainly with Casuarinaceae trees

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Abstract

The diversity is reviewed of Phlaeothripinae in Australia with unusually long or convoluted maxillary stylets. This comprises a total of 28 species in eight genera, including *Enigmathrips carnarvoni* gen et sp.n., *Adrothrips latrarei* sp.n., *A. lihongae* sp.n., *A. madiae* sp.n., *A mitcheli* sp.n., *A. vernoni* sp.n., and *A. westoni* sp.n., also *Heligmothrips exallus* sp.n., *H. macropus* sp.n., *H. narrabri* sp.n. and *H. xanthoskelus* sp.n., and *Iotatubothrips daguilari* sp.n. Among Phlaeothripinae, such exceptionally long feeding stylets are known only from Australia and have evolved independently within the unrelated genera *Adrothrips* and *Heligmothrips* in association with the green branchlets of Casuarinaceae species. A few species appear to have diverged in their feeding habits and have adapted to fungal-hyphal feeding on the trunks of trees.

Key words: elongate feeding stylets, phytophagy, host-plant specificity, systematic relationships

Introduction

The maxillary stylets of thrips in the sub-family Phlaeothripinae vary greatly in length between taxa. Among species of Sophiothrips and Williamsiella these stylets are as short as those of the Thripidae and are scarcely retracted into the head capsule (Mound & Tree 2014 2015). In contrast, the stylets of many common fungus feeding Phlaeothripinae, such as species of Hoplandrothrips and Strepterothrips, are elongate and retracted deeply into the head, even to within the eyes (Mound & Tree 2022). However, the stylets of species discussed here are often far longer, arranged into convolutions or even coils, such that in Adrothrips intermedius they are longer than the body length (Mound 1970). Amongst Phlaeothripinae, these modifications have not been reported from any part of the world other than Australia, and on this continent species with these convoluted stylets are found predominantly on trees of the genera Casuarina and Allocasuarina. However, a few species are known only from a few specimens that have been taken by insecticide barkspraying on either a Eucalyptus or an Acacia tree. Such species are included in this review because of their complex stylets, although currently it is not possible to know their true host plants and feeding sites. The radiation in Australia of plant-feeding Phlaeothripinae on trees of Casuarina and Allocasuarina is remarkably extensive. This radiation is interpreted here as comprising a minimum of eight genera and 28 species, including 12 new species and one new genus that are described below. This contrasts with the even larger radiation in Australia of plant-feeding Phlaeothripinae on the genus Acacia [Fabaceae]. In that radiation, Crespi et al. (2004) recognised over 250 species in 30 genera, with a biological diversity involving gall-inducing and nest-building species, as well as kleptoparasitic species that usurp fresh galls and nests, and many invasive species that breed in old and

abandoned galls and nests. These radiations contrast with the absence of leaf-feeding Phlaeothripinae on any of the 1000 species of the genus *Eucalyptus* [Myrtaceae], the most species-rich plant genus in Australia, also the absence of such thrips from the foliage of the many endemic Proteaceae.

The plant family, Casuarinaceae, comprises four genera and just over 90 species, and most of these species are found only in Australia. One genus, *Ceuthostoma*, comprises two species and these are known only from Borneo and New Guinea. *Gymnosperma* comprises less than 20 species particularly in the Indonesian archipelago and New Caledonia, but with one species in Australia, in the Daintree rainforest of northern Queensland. However, the genus *Allocasuarina* is endemic to Australia, and the 60 included species occur mainly in the southern parts of this continent. In contrast, the genus *Casuarina* includes less than 20 species, and is found widely across this continent. A few species of *Casuarina* occur on Pacific islands as well as in southeast Asia and even the east coast of Africa, but nothing is known of the thrips fauna on any non-Australian Casuarinaceae. In Australia, species identification within *Casuarina* and *Allocasuarina* can be difficult, and few identified species of these trees have been sampled for thrips. The Phlaeothripinae radiation reported here as feeding on the tissues of these trees is represented by several species that are based on single or few specimens, suggesting that the species diversity may be considerably higher.

In Australia, almost all the Thysanoptera species that are associated with the living tissues of Casuarinaceae trees are members of the subfamily Phlaeothripinae. The two known exceptions are both species of Thripidae, *Pseudanaphothrips casuarinae* and *Scirtothrips casuarinae* (Mound & Tree 2020). However, in decaying leaf-litter beneath many *Casuarina* trees a species of Phlaeothripidae-Idolothripinae, *Carientothrips casuarinae*, is commonly found breeding and feeding on fungal spores (Eow *et al.* 2014).

Host associations. The plant-feeding phlaeothripines on Allocasuarina and Casuarina trees occupy a range of different habitats. Species of Heligmothrips, also some species of Adrothrips and Akthethrips, occur on the living tissues of the green branchlets. These species have unusually elongate, often convoluted or even coiled, maxillary stylets (Figs 11–19; 51–59). Presumably these elongate stylets are an adaptation to feeding on the living cells of these branchlets (Fig. 1) that are protected by robust sclerenchyma. The living cells and stomata are concealed within the longitudinal grooves of the green branchlets and are further protected by hairs (Mound 1970). However, one species of Adrothrips has been found breeding within a small woody gall on a young branch of Allocasuarina verticillata, and this habit is possibly more widespread among species of this genus. Certainly, the bizarre diversification of the tenth abdominal segment in some species of Adrothrips might suggest some form of protection against predatory ants by a species living in a cavity, as in Dactylothrips on Acacia branches (Crespi et al. 2004). In contrast, the three known species of the genus *Iotatubothrips* induce substantial woody galls on young branches of particular Casuarina species, and rear within each gall a colony of winged and wingless adults. These galls are invaded by Phlaeothripinae belonging to two further genera, *Phallothrips* and *Thaumatothrips*, and these thrips behave as phytophagous kleptoparasites that fully usurp the *lotatubothrips* galls (Mound et al. 1998). One species, Xyelethrips quadritibia from sub-tropical Queensland, was presumed by Mound (1970) to live on Casuarina because of the convoluted stylets. However, this species is here considered to be more likely to be fungus-feeding on the bark of trees. Similarly, the species described here as Adrothrips latrarei sp.n. is known only from six micropterae taken from the trunk of a Eucalyptus tree in southeastern Queensland. Despite the collecting data, this species shares character states with the other species of Adrothrips. Even more confusing is the new genus and species with convoluted stylets described below from sub-tropical Queensland, Enigmathrips carnarvoni, that is known only from five females taken from the bark of Acacia harpophylla. These three species further suggest that the diversity of the Thysanoptera fauna in Queensland sub-tropical forests remains inadequately explored.

Population structure. Species considered here that are associated with woody galls, such as members of *Iotatubuthrips*, *Phallothrips* and *Thaumatothrips*, occur locally as large populations. Similarly, populations of *Heligmothrips* species are sometimes considerable at any one locality. In contrast, populations of some species have been found to be highly variable from year to year, presumably in response to seasons as well as rainfall and temperature variations. Some species of *Adrothrips*, although widespread, are collected infrequently and only in very low numbers, despite intensive collecting efforts where single individuals are often found. Presumably, as with many Thysanoptera species, populations sometimes increase rapidly for short periods, but have extended periods with very low populations. Discovering the biology of these small, tree-living insects is particularly difficult.

Systematic relationships. The genera Heligmothrips and Thaumatothrips are presumably derived from within the worldwide Liothrips-lineage of leaf-feeding Phlaeothripinae, with Heligmothrips particularly closely related to the Teuchothrips complex (Mound & Goldarazena 2022). However, Adrothrips species share character states with members of the Rhopalothripoides group that live on the stems of Acacia trees, and Iotatubothrips is presumably related to Adrothrips. Thus, the elongate and coiled maxillary stylets of Adrothrips and Heligmothrips species have

evolved independently. The elongate stylets of the genus *Xyelethrips* are also independently derived, as this genus is considered a member of the distinctive tribe Plectrothripini within the Phlaeothripinae. More problematical is the relationship of *Enigmathrips* gen.n. diagnosed here for a single new species that was taken from a *Eucalyptus* trunk. This has elongate and convoluted maxillary stylets that are similar in arrangement to some species of *Adrothrips*, but the sensorium on antennal segment II is placed on the basal half of that segment. Despite this, the rest of the antenna is typical of species in the *Liothrips*-lineage. Although the narrowed abdominal tergite II of *Enigmathrips* is sometimes considered typical of Plectrothripini, this tergite is also eroded laterally in some *Adrothrips* species. Moreover, the only known species of the genus *Akthethrips* shares the condition with Plectothripini of the sensorium on antennal segment II not being on the distal half of that segment.



FIGURE 1. *Casuarina cunninghamiana* - transverse sections of green branchlet indicating protection of chlorophylous tissue within longitudinal grooves (from Mound, 1970).

Maxillary stylet orientation. The position of the stylets within the head seems to be highly specific to each species, but interpreting this character state requires great care during the processes of slide-mounting to minimize any disruption in position of the stylets. In most genera this has proved not to be a great problem, but the situation amongst some species of *Heligmothrips* remains difficult to interpret. For these species, series of specimens will be needed from multiple identified host plants before the complex species group associated with the names *H. erinaceus* and *H. gracilior* can be fully resolved.

Depositaries, abbreviations and acknowledgements

Holotypes of new species described here are deposited in the Australian National Insect Collection, CSIRO, Canberra (ANIC). Some paratypes and many identified specimens are deposited in the Queensland Primary Insect Collection, Brisbane (QDPC). Abbreviations are used for the two common genera of Casuarinaceae mentioned here: *A*. for *Allocasuarina* and *C*. for *Casuarina*. For the major body setae the usual abbreviations are used; pronotal setae: am for anteromarginals, aa for anterangulars, ml for midlaterals, epim for epimerals, pa for posteroangulars. Tergite IX setae S1 and S2 for the dorsal and dorsolateral pairs of setae. We are particularly grateful to Vernon and Madeline Wells for facilitating thrips collecting on Kangaroo Island. Mark Schutze kindly organized the loan of large numbers of microscope slides from the Queensland Primary Insect Collection, Bogor Road, Brisbane. Karin Koch at the Brisbane Museum, Queensland, kindly facilitated the loan to Canberra of a Girault type slide. The Zootaxa editor and two reviewers provided many comments to help improve the clarity of this presentation.

Key to Phlaeothripinae genera associated with Casuarinaceae

1.	Antennal segment VIII slender and sharply constricted to narrow basal pedicel (Fig. 77); antennal segment II with sensorium on basal half of segment; mouth cone pointed and extending to (or almost to) mesosternum (Fig. 74)
	Antennal segment VIII short with broad base; antennal segment II with sensorium usually on distal half of segment; mouth cone shorter, rarely extending across prosternum
2.	Antennal segment IV with 2 sense cones, III without sense cones (rarely with only 1); fore wing without duplicated cilia or micropterous
	Antennal segment IV with 3 sense cones (rarely with only 2), III with one sense cone; fore wing usually with duplicated cilia, rarely micropterous.
3.	Antennal segment VI broadly truncate at apex, VII scarcely narrowed at base (Figs 2–9); maxillary stylets crossing over each other in head or at least touching medially (Figs 11–19)
	Antennal segment VI with apex slightly narrowed, VII clearly narrowed to base (Fig. 72); maxillary stylets more widely separated
4.	Antennal segment III without sense cones; female abdominal segment IX without sclerotised fustis; postocular setae long in macropterae, short in micropterae
	Antennal segment III with one sense cone; female abdominal segment IX with fustis well developed; post ocular setae always minute
5. 	Fore femora of both sexes with row of tubercles on inner margin (Fig. 47)
6.	Head of females with inter-antennal projection about as long as antennal segment I (Fig. 40), males with this projection only half as long as antennal segment I
-	Head not produced between bases of antennal segments
7.	Head elongate, more than 1.5 times as long as wide (Fig. 44), with mouth cone acute, extending across prosternum; mesopresternum reduced to small median sclerite (Fig. 45); tergite II strongly eroded laterally; antennal segment II with sensorium on basal half of segment (Fig. 43); fore wing when present broad but without duplicated cilia and tergites without wing-retaining setae
	Head wider than long, rarely more than 1.1 times as long as wide, mouth cone not extending across prosternum; mesopresternum transverse or reduced to two lateral triangles (Figs 64–66); tergite II complete laterally; antennal segment II with sensorium on distal half of segment; fore wing rarely absent, with duplicated cilia

Adrothrips Moulton

Adrothrips Moulton, 1942: 4. Type species Adrothrips aureus Moulton, by monotypy.

Described as monotypic, this genus was subsequently revised to include five species (Mound 1970), although seven more new species are described below. There is considerable structural diversity among these 12 species, including the length of the maxillary stylets, and in females the form of the tube, the tenth abdominal segment. This terminal abdominal segment is simple and tubular in most of the species, but unusually short in one species (vernoni sp.n.), and with the basal half broadly swollen in four species (acanthus, aureus, cotteri and mitchelli sp.n.). However, the length of the maxillary stylets is not correlated with the form of the tube, such that *aureus* and *cotteri* have a similar remarkable tube (Figs 33-34), but *cotteri* has shorter stylets that are similar to those in *vernoni* (Figs 13, 20) in contrast to the long stylets of aureus (Fig. 12). Ten of the species lack a sense cone on antennal segment III but in two species this sense cone is present. However, these two are also probably not closely related, because the maxillary stylets are rather short in *lihongae* sp.n. but arranged into coils in *latrarei* sp.n. (Figs 15–16). The variation in stylet lengths among the various species is possibly related to differences in the feeding sites, such that the species with exceptionally long and coiled stylets live on green branchlets, as discussed by Mound (1970). However, at least one of the species with shorter stylets (vernoni sp.n.) seems to live either in galls or on the split surface of young woody stems. The genus Adrothrips is most likely related to the complex of Rhopalothripoides species that live on the split stems of young branches of Acacia species (Crespi et al. 2004).

Diagnosis. Small pale, bicoloured or light brown, macropterous or micropterous Phlaeothripinae, usually with exceptionally long maxillary stylets. Head little longer than wide; postocular setae small and capitate; maxillary

stylets deeply retracted into the head, usually crossing each other or rarely touching medially, usually with one or more convolutions near base of head. Antennae 8-segmented; III usually with no sense cones but sometimes with 1, IV with 2 ventral sense cones; V slightly asymmetric at apex; VI broadly truncate at apex, VII not narrowed at base; VIII small. Pronotal major setae small with expanded apices, usually all 5 pairs present but am and ml sometimes not developed; notopleural sutures complete. Prosternal basantra absent, mesopresternum transverse, or reduced to two sclerites, or absent; metathoracic sternopleural sutures long, sometimes eroded. Mesonotal midlateral setae very small, apex expanded. Metanotum with several pairs of small setae. Fore tarsal tooth present in female, usually present in male; fore tibia rarely with an apical tubercle. Fore wings evenly wide, without duplicated cilia; 3 short sub-basal setae present with expanded apices. Pelta broadly triangular; tergites II–VII usually with 2 pairs of sigmoid wing-retaining setae; posteroangular setae small on tergites II–VI; tergite IX setae S1 and S2 short and capitate, S3 acute; tube shorter than head, sometimes strongly reticulate and expanded. Male tergite IX setae S2 similar to setae S1; sternite VIII with no pore plate, but median sternites sometimes with transverse band of specialised reticulation.

Key to Adrothrips species

1.	Antennal segment III with one long sense cone, this segment about 2.5 times as long as wide, (Figs 5–6); pronotal anteromarginal and midlateral setae minute
	Antennal segment III with no sense cones, this segment usually less than 2.0 times as long as wide; pronotal anteromarginal and midlateral setae small but capitate
2.	Antennal segment III simple at base (Fig. 6); maxillary stylets broadly crossing over each other with one large posterolateral loop (Fig. 15)
	Antennal segment III with sharp-edged sub-basal disc (Fig. 5); maxillary stylets with about three posterolateral coils (Fig. 16)
3. 	Maxillary stylets with posterolateral coils or convolutions (Figs 14, 17–18)
4. 	Head about 1.8 as long as wide (Fig. 17), vertex with weak longitudinal reticles with no internal markings <i>madiae</i> sp.n . Head as wide as long, with vertex reticulate and reticles having internal markings
5.	Maxillary stylets with 3-6 clearly defined coils posterolaterally (Fig. 14); head largely yellow, metanotum with U-shaped brown marking
	Maxillary stylets with two irregular convolutions posterolaterally (Fig. 18); head metanotum largely brown with median area pale
6. 	Maxillary stylets widely crossing over each other medially in head (Figs 11–12)
7. 	Tergites VIII–IX posterolaterally with several short stout spines (Fig. 32)
8. -	Antennal segment III usually at least 2.0 times as long as wide (Fig. 2); fore tibia with papilla-like tubercle near inner apex [tube of female strongly sculptured and angulate medially with distal third sharply narrower (Fig. 33)]
9.	Female with tube strongly sculptured on basal half (Fig. 36); antennal segment III evenly narrowing to basal pedicel (Fig. 10)
-	Female with tube without sculpture, evenly narrowing to apex (Fig. 39); antennal segment III sharply narrowed to basal pedicel (Fig. 8)
10.	Antennal segment III at least 1.5 times as long as wide (Fig. 3); tube of female sharply constricted on distal half with expanded basal half strongly sculptured (Fig. 34); fore tibia of female with sub-apical tubercle on inner margin; mesopresternum of female fully developed and transverse
	Antennal segment III short, as wide as long (Fig. 8); female with tube short, weakly constricted medially (Fig. 38); fore tibia without sub-apical tubercle; mesopresternum strongly eroded

Adrothrips akanthus Mound

(Figs 11, 32)

Adrothrips akanthus Mound, 1970: 446

Described from three female and three male macropterae taken in Queensland near Goondiwindi, also one male collected on the same day but in northern New South Wales near Moree. The only other known specimens are listed below and include females from South Australia. The antennae and pelta are similar to those of *cotteri*, but the head is different in having the maxillary stylets broadly crossing each other (Fig. 11). Females have a single pair of long, sigmoid wing-retaining setae on tergites II–V, but males on II–VII. Tergites IV–VII of females have double transverse rows of short stout setae (Fig. 32), and similar setae are on the basal half of the tube and the posterolateral angles of the ninth tergite. The mesopresternum is narrowed medially where the anterior margin of the mesoeusternum projects forwards.

Specimens studied. holotype female macroptera, **Queensland**, Goondiwindi 10km north, with paratype male from *Casuarina ?glauca*, 16.vii.1968; Meeandara, 1 female from *C. glauca*, iv.2000. **New South Wales**, Goondiwindi 30km South, 1 female 2 males from *C. cristata*, 20.v.2022; Moree 40km North, 2 females 1 male from *C. cristata*, 20.v.2022. **South Australia**, Whyalla 30km north, from *Casuarina pauper*, 2 females 26.x.1996, 1 female 14.iii.1997.

Adrothrips aureus Moulton

(Figs 2, 12, 22, 33)

Adrothrips aureus Moulton, 1942: 5

Although based originally on three females taken 16.v.1931 at Ivanhoe in central New South Wales, and reported by Mound (1970) from Moree, this species has now been seen widely across Australia. In females, the tenth abdominal segment is strongly sculptured with the basal half broad and the distal half sharply narrower (Fig. 33), whereas in males it is a typical tube although reticulate in basal half. Antennal segment V has the apex strongly asymmetric in both sexes (Fig. 2), but although the mesopresternum of females is fully transverse in males it is variably eroded. The fore tarsus has a stout tooth in both sexes, and females have a prominent papilla on the inner apical margin of the fore tibia although this is smaller in males. One of the host plants of this thrips, *Casuarina obesa*, has a strongly discontinuous distribution, being common in Western Australia and also in eastern South Australia plus western Victoria.

Specimens studied. This species has been found in all five of the Australian mainland States. **Victoria**, Mildura 50km west, 2 males from *C. pauper*, 25.iv.1995. **South Australia**, near Renmark, 2 females in intercept traps, iii–v.1995; Iron Baron near Whyalla, 1 female from *C. pauper*, 12.vi.1997. **Western Australia**, Murchison River Crossing, from *C. obesa*, 5 females, 2 males, 25.iv.1997, 1 female, 12.x.2003; Northampton 60km east, 2 males from *C. obesa*, 25.iv.1997; Gingin 60km north of Perth, 1 female from grass, 29.ix.1995. **New South Wales**, Balranald 20–40km west, 2 females, 1 male from *Casuarina obesa*, 14.iv.2022; Moree 40km North, 3 females from *C. cristata*, 20.v.2022. **Queensland**, Dalby, Lake Broadwater, from *C. cristata* foliage: 4 females, 2 males 8.iii.2006, 1 female 1 male, 7.ix.2009; same locality, 1 female, 1 male from *Acacia harpophylla*, 19.vii.1995; Moonie 10km East, 1 female from *C. cristata*, 20.v.2022; Moonie, 20km East, 1 male from *C. cristata*, 20.v.2022; Moonie 10km South, 1 female from *C. cristata*, 20.v.2022; Charters Towers, 1 female that is unusually small and lacks the fore tibial papilla-like tubercle that is typical of *aureus*.

Adrothrips cotteri Mound (Figs 3, 13, 28)

Adrothrips cotteri Mound, 1970: 444

Described from two female and three male macropterae collected near Canberra, 9.vi.1968, no further specimens

have been found at the type locality despite repeated searching. However, as indicated in the list below, this species has been found more recently from three widely separated areas in eastern Queensland, between Brisbane and Charters Towers. The tergites and tube of females are remarkably similar to those of female *aureus*, and the fore tibia bears a similar papilla-like tubercle at the inner sub-apex. However, the maxillary stylets are shorter and do not cross over each other (Fig. 13). The tube of males is straight sided but the basal half bears reticulation that is similar to that of females. Antennal segment V has the apex asymmetric (Fig. 3), and the mesopresternum is fully transverse (Fig. 28).



FIGURES 2–10. Adrothrips species antennae. (2) aureus; (3) cotteri; (4) intermedius; (5) latrarei; (6) lihongae; (7) madiae; (8) vernoni; (9) westoni; (10) mitchelli.

Specimens studied. Holotype female macroptera, **Australian Capital Territory**, Casuarina Sands, from *C. cunninghamiana*, 9.vi.1968. **Queensland**, Charters Towers 200km north, 1 female, 1 male from *Casuarina*, 3.vii.1995; Mt Malloy 25km north, 1 male from *Casuarina*, 6.vii.1995; Carnarvon National Park, Chanin River Crossing, 14.x.2014, 1 female from *Casuarina* lves; Brisbane, The Gap, 1 female from *Casuarina*, 30.x.2007.

Adrothrips intermedius (Bianchi)

(Figs 4, 14, 23, 35)

Scopaeothrips intermedius Bianchi, 1945: 254

This species was described originally from New Caledonia, from one female and three males taken on the indigenous tree *Casuarina collina*. The holotype and one male were studied subsequently, and Mound (1970) recognised and

illustrated the remarkable condition of the elongate and multiply coiled maxillary stylets (Fig. 14). As indicated below, it is a widespread species in Australia that varies in size; specimens in the northern tropical area are distinctly paler, and specimens in the far West darker with longer antennae. However, there are no consistent structural differences among the samples listed here, and they share the following character states:

Macropterae. Body largely yellow and varying in extent of brown markings; head with light brown area posteromedially, pronotum with pair of dark areas; mesonotum dark laterally; metanotum variably brown with paler area anteromedially (Fig. 23); metaepimera dark; tergites II-VII with pair of dark areas extending across anterior margin; tube varying from dark to almost yellow; legs with light brown shadings medially on femora and tibiae; antennal segments I-III paler than IV-VIII; fore wings clear, all major setae translucent. Head about as long as wide, genae convex; postocular setae acute to weakly capitate; vertex reticulate with markings internal to each reticle. Maxillary stylets retracted to posterior margin of eyes, crossing over each other medially then again posterior to occipital ridge, each in a coil posterolaterally before entering mouth cone. Both of the coils comprise several rings (Fig. 14), and the number varies between localities; in most populations 4–5 but with up to 6 in Western Australia and only 2-3 in some specimens from Carnarvon Gorge, Queensland. Antennal segment III 1.4-1.8 as long as wide with no sense cone, IV with 2 sense cones, apex of V weakly asymmetric with one short stout sense cone and one small thin sense cone on inner apical margin (Fig. 4). Pronotum extensively but weakly reticulate medially, reticles with inner markings, setae weakly capitate. Metanotum reticulate, reticles with internal markings, bearing 20–24 small setae (Fig. 23). Fore tarsus with tooth, large males with tooth larger than small males. Prosternal ferna transverse; mesopresternum variable with pair of lateral triangles sometimes extending medially; mesoeusternum anterior margin transverse but convex medially in large male; metathoracic sternopleural sutures long and slender. Pelta broadly bell-shaped; tergites extensively reticulate, reticles with internal markings, II-VII each with two pairs of wing-retaining setae but posterior pair much stronger than anterior pair on each tergite; tergite IX setae capitate, shorter than basal width of tube; tube broader near base than in apical third (Fig. 35). Sternites II-VII of larger males with transverse band of irregular specialised reticulation.

Specimens studied. Specimens identified as *A. intermedius* have been studied from many areas across Australia. In the **Australian Capital Territory** it lives on *C. cunninghamiana*. **New South Wales** in areas near the coast (Batemans Bay, Sydney, Gosford, Pottsville) it lives on *C. glauca*. **South Australia**, around Whyalla, it lives on *C. glauca*. **Victoria**, at Mildura populations have been found on *C. pauper* but also on *Allocasuarina luehmanni*. **Queensland** in the southeast (Dalby, Moonie) the species lives on *C. cristata*, but at Noosaville it has been taken from *C. equisetifolia*. **Western Australia**, at various sites near the West coast (Murchison River crossing southeast of Kalbarri; Northampton 60km east; Gingin north of Perth; East Freemantle) this species has been found on *C. obesa*. The specimens from these western localities have antennal segment III more elongate than any specimens from eastern localities (1.8 times as long as wide, in contrast to 1.4–1.6 times). They also usually have the metanotum more extensively brown.

Micropterae, of both sexes, have been studied. Samples from Carnarvon Station and Charters Towers (Queensland), as well as from Bourke (New South Wales), included a few micropterae of both sexes. At various sites across Australia, males have been found with the frons produced medially between the eyes into a small papilla, and this in some males is enlarged and prolonged ventrally. As with the presence of specialised reticulate areas on the sternites of males, this structure on the frons is associated with, but not closely correlated with, body size.

Adrothrips latrarei sp.n. (Figs 5, 16, 24, 29)

Female microptera. Body uniformly light brown, antennal segments III–VI variably yellowish near base; legs brown with apex of fore tibiae and all tarsi yellow; major setae all pale. Head longer than wide, eyes larger dorsally than ventrally, ocelli reduced; postocular setae small and acute or weakly capitate; vertex with weak transverse narrow reticulation. Maxillary stylets retracted almost to eyes, close together medially, each with three coils posterolaterally before entering the mouth cone (Fig. 16). Antennae robust, segment III with one sense cone about half as long as apical width of segment, basal pedicel produced into strong ring (Fig. 5); segments IV and V each with 2 sense cones; apex of V almost symmetrical, of VI broad; VIII small and closely joined to VII. Pronotum with weak, transverse sculpture only near posterior margin, anteromarginal setae minute, midlaterals small but capitate.

Metanotum irregularly reticulate, without internal markings, bearing up to 16 small setae (Fig. 24). Mesopresternum fully transverse, projecting forwards medially (Fig. 29); ferna almost meeting medially. Fore tarsal tooth small, fore tibiae simple. Fore wing lobe usually shorter than thorax width but sometimes slightly longer. Pelta D-shaped to triangular, weakly reticulate (Fig. 24); tergites with transverse row of fine setae medially, anterior pair of wing-retaining setae reduced on each tergite, both pairs reduced or absent on VII; tergite IX setae capitate and shorter than basal width of tube; tube rather slender, twice as long as basal width.



FIGURES 11–19. Adrothrips heads. (11) acanthus; (12) aureus; (13) cotteri; (14) intermedius; (15) lihongae; (16) latrarei; (17) madiae; (18) systemus; (19) westoni male.

Measurements (holotype female in microns). Body length 2500. Head, length 260; width medially 230; po setae 25. Pronotum, length 175; width 275; major setae – am 12, aa 35, ml 25, epim 40, pa 30. Fore wing length 230; sub-basal setae 25. Tergite IX setae S1 60, S2 85. Tube, basal width 85, length 185. Antennal segments III–VIII length 70, 65, 65, 70, 25, 25.

Male microptera. Slightly smaller, but very similar in colour and structure to female; tergite IX setae S2 slightly longer than setae S1.

Specimens studied. Holotype female microptera, **Queensland**, Brisbane, Mt Glorious, Dundas Road, from barkspray on *Eucalyptus* trunk, 29.x.2008 (DJ Tree 756), in ANIC.

Paratypes 2 females, 3 males collected with holotype; Queensland, Carnarvon N.P., Mt Moffat Consuelo Tableland, 2 females from barkspray on *Eucalyptus*, 17.i.2013; in ANIC and QDPC.

Comments. Among members of this genus this species shares only with *lihongae* **sp.n**. the presence of a sense cone on antennal segment III. In contrast to that species the maxillary stylets are very long and arranged into three coils posterolaterally (Fig. 16), the pedicel of antennal segment III has a strong sub-basal ring, the surfaces of the head and thorax are not reticulate, and the body is uniformly brown. The only available specimens were taken by insecticide fogging on the trunk of *Eucalyptus* trees, and the specific epithet refers to this finding place.

Adrothrips lihongae sp.n.

(Figs 6, 15, 30)

Female macroptera. Body light brown, with pale markings behind eyes and laterally on pronotum and tergites II–IV; antennal segment III yellowish on basal half; tarsi yellow, also apices of hind tibiae and inner margin of hind femora; tube darkest at apex; fore wings pale; major setae all pale except wing retaining setae on tergites II and III. Head longer than wide, eyes well developed, postocular setae minute; vertex transversely reticulate with markings internal to each reticle. Maxillary stylets retracted into eyes, crossing over near ocelli then re-crossing at occipital ridge, each with one large circle before extending parallel to each other into the mouth cone (Fig. 15). Antennae rather slender, segment III simple at base (Fig. 6) and with a single sense cone that is almost as long as apical width of segment, IV with 2 sense cones, apex of V weakly asymmetric. Pronotum with weak, complicated reticulation, anteromarginal and midlateral setae minute. Metanotum irregularly reticulate, reticles with internal markings, bearing about 20 small setae. Mesopresternum complete but weakly sclerotised and slender medially where the anterior margin of the mesoeusternum projects forwards (Fig. 30). Fore tarsal tooth small, fore tibiae simple. Fore wing sub-basal setae minute. Pelta reticulate; anterior pair of wing-retaining setae reduced on each tergite, both pairs reduced on VII; tergite IX setae capitate and shorter than basal width of tube; tube twice as long as basal width, similar to *latrarei*.

Measurements (holotype female macroptera in microns). Body length 2300. Head, length 300; width medially 250; po setae 20. Pronotum, length 165; width 320; major setae – am 12, aa 25, ml 12, epim 25, pa 25. Fore wing length 750; sub-basal setae 12. Tergite IX setae S1 35, S2 50. Tube, basal width 75, length 150. Antennal segments III–VIII length 75, 70, 60, 60, 25, 25.

Female microptera. Colour similar to macropterae but antennal segment III and tergites more extensively brown; base of antennal segment III more robust and less tapered than macropterae; head with ocelli reduced; pronotal am setae not distinguished from discal setae; metanotum almost transverse, with discal setae weakly capitate; fore wing lobe about 0.3 as long as thorax width; pelta wider than long, almost D-shaped; tergites with about 20 setae in median transverse row.

Specimens studied. Holotype female macroptera, **South Australia**, Coorong, from base of grasses, 3.x.2013 (Dang Lihong 77), in ANIC.

Paratypes: **South Australia**, Ngarkat Conservation Park, 1 female macroptera from dead wood, 4.x.2013 (DJT 1678); Mt Remarkable, Alligator Lodge, 1 female microptera under bark of dead *Eucalyptus*, 14.iii.2011 (G. Monteith), in QDPC. **Western Australia**, 60km northeast of Narrogin, 1 female macroptera by insecticide fogging of *Eucalyptus* tree, x.2006 (A. Lyons), in ANIC.

Comments. Within the genus, this species shares only with *latrarei* **sp.n**. the presence of a sense cone on the third antennal segment, but as indicated above, as well as in the key, these two differ considerably in structure and colour. The mesopresternum is particularly similar to that of *akanthus*. None of the four available specimens

have been collected from any she-oak species, each of them being taken by beating or insecticide fogging on dead branches. As with some other members of *Adrothrips*, this species apparently is widely distributed across this continent. The female from Ngarkat, not far from the type site, is considerably smaller than the holotype (body length 1950 microns).

Adrothrips madiae sp.n.

(Figs 7, 17, 25)

Female microptera. Body largely yellow, head weakly shaded posteromedially, pronotum with pale brown area medially, mesonotum and metanotum with brown areas, meta-epimera darker; tergites II-VII each with transvers brown band on anterior half; tube dark brown with base yellow; legs mainly yellow, mid and hind femora and tibiae with brown shadings; antennal segments I-III mainly yellow, remaining segments increasingly dark. Major setae all translucent. Head about 1.6 as long as wide, genae parallel (Fig. 17); postocular setae small and capitate but distant from eye margin; vertex weakly reticulate. Maxillary stylets retracted into basal third of head, close together medially, with two flexures forming a figure-of-eight before entering mouth cone. Antennal segment III with no sense cone, IV with 2 stout sense cones, apex of V slightly constricted and symmetric with one short stout sense cone, V-VI each with narrow pedicel (Fig. 7). Pronotum about as long as wide and narrower than prothorax (Fig. 17), with distinct median longitudinal apodeme but little reticulation, all five pairs of major setae small and capitate. Metanotum reticulate, reticles with few internal markings, bearing 10-12 small setae (Fig. 25). Prosternal ferna with anterior margin almost transverse; mesopresternum consisting of two lateral triangles; metathoracic sternopleural sutures long and slender. Fore legs massive, tarsal tooth stout, about as long as tarsal width. Fore wing lobe very small with 2 sub-basal setae. Pelta broadly triangular, reticulate; tergites II-VII each with only posterior pair of wing-retaining setae, these are sometimes only weakly developed; tergite IX setae capitate and about as long as basal width of tube; tube weakly constricted medially and at apex.

Measurements (holotype female in microns). Body length 1800. Head, length 225; width medially 125; po setae 12. Pronotum, length 200; width 220; prothorax width across coxae 350; major setae – am 12, aa 12, ml 15, epim 25, pa 20. Fore wing length 65; sub-basal setae 12. Tergite IX setae S1 50, S2 60. Tube, basal width 55, length 105. Antennal segments III–VIII length 40, 40, 38, 50, 25, 20.

Male microptera. Closely similar to female but smaller.

Specimens studied. Holotype female microptera, **South Australia**, Kangaroo Island, American River, from *Allocasuarina verticillata*, 3.iv.2021 (LAM 6482), in ANIC.

Paratypes: Kangaroo Island, 4 females, 1 male taken with holotype; same site and host, 1 female, 31.iii.2021, 1 female, 29.xi.2021; Stokes Bay, 1 female from same host, 30.xi.2021; Destrey's Bay Road, 1 male from *Allocasuarina muelleriana*, 1.xii.2021. **Australian Capital Territory**, Canberra, Weston, Oakey Hill, 1 female from *Allocasuarina verticillata*, 29.xi.2002.

Comments. This is an unusually pale species with a relatively slender head and pronotum. The stylets are arranged in a similar pattern to those of *systemus*, but in that species the body surface is much more strongly sculptured and the tube slightly swollen in the basal third (Fig. 37).

Adrothrips mitchelli sp.n. (Figs 10, 21, 36)

Female macroptera. Body brown, tube darkest with tarsi, apices of tibiae and antennal segment III paler; fore wings clear. Head about as long as wide, postocular setae capitate; vertex transversely reticulate with markings internal to each reticle. Maxillary stylets retracted into eyes, crossing over near ocelli then re-crossing at occipital ridge, with one flexure before entering the mouth cone (Fig. 21). Antennal segment III short with no sense cone, IV with 2 sense cones, apex of V asymmetric with one short stout sense cone (Fig. 10). Pronotum with weak, complicated reticulation, all five pairs of major setae short and capitate. Metanotum irregularly reticulate, reticles with internal markings, bearing many small setae. Mesopresternum reduced to two weak triangles. Fore tarsal tooth scarcely visible, reduced to a small lobe on the inner basal third of the tarsus. Fore wing with 2 capitate sub-basal setae. Pelta

elongate triangular, reticulate; posterior pair of wing-retaining setae long and placed laterally on tergites II–VI, anterior pair reduced on each tergite, both pairs reduced on VII; tergite IX setae capitate and shorter than basal width of tube; tube sculptured, much broader in basal than in distal third (Fig. 36).



FIGURES 20–27. Adrothrips heads, metanotum & pelta. (20) vernoni holotype; (21) mitchelli holotype; (22) aureus; (23) intermedius; (24) latrarei; (25) madiae; (26) vernoni; (27) systemus.

Measurements (holotype female in microns). Body length 1640. Head, length 170; width medially 160; po setae 12. Pronotum, length 115; width 200; prothorax width across coxae 270; major setae – am 10, aa 12, ml 12, epim 25, pa 20. Fore wing length 130; sub-basal setae 12. Tergite IX setae S1 30, S2 40. Tube, basal width 65, maximum width 75, length 90. Antennal segments III–VIII length 30, 37, 37, 45, 25, 20.

Specimen studied. Holotype female macroptera, **New South Wales**, Trangie, from *Acacia pendula*, 8.xii.2001 (LAM 4065) in ANIC.

Comments. The only available specimen is uncleared, such that some details are not visible. The head and stylets are similar to *aureus* but dark brown (Fig. 21) but the form of the tenth abdominal segment is unique in this genus (Fig. 36), and the fore tarsal tooth is reduced to a very small swelling on the inner basal third of the tarsus.

Adrothrips systenus Mound

(Figs 18, 27, 37)

Adrothrips systemus Mound, 1970: 451

Described originally from three female and two male micropterae taken at Moree from *Casuarina glauca*, this species remains known from few specimens. The maxillary stylets of the slide-mounted type specimens are possibly slightly out of their natural position, and probably are more deeply retracted into the head capsule in life (Fig. 18). The mouth cone is long and pointed, and postero-lateral flexures of the stylets are rather similar to the condition in *madiae* **sp.n**., each with two curves twisted into an irregular figure-of-eight. Antennal segment V apex is almost symmetrical, the prosternal ferna are slender, transverse and almost continuous medially, and the mesopresternum is eroded to two slender lateral triangles with the mesoeusternal border transverse. The metanotum and tergites bear many short blunt pale setae (Fig. 27), and the tube is slightly enlarged in the basal third (Fig. 37).

Specimens studied. Holotype female microptera, **New South Wales**, Moree 50km north, from *Casuarina glauca*, 16.vii.1968, in ANIC; **Queensland**, Dalby, Broadwater Lake, from *Casuarina cristata*, 1 male microptera, 8.iii.2006, in QDPC.

Adrothrips vernoni sp.n.

(Figs 8, 20, 26, 31, 38)

Female macroptera. Body brown, basal half of tube usually paler; tarsi and apices of tibiae yellow; antennal segment III and apex of II paler than remaining segments; fore wing pale and weakly sclerotised; major setae all translucent. Head longer than wide with posterior margin slightly eroded; postocular setae capitate usually reaching to eye margin; vertex weakly reticulate. Maxillary stylets retracted to eyes, parallel or slightly crossing over each other medially, with one flexure before entering mouth cone (Fig. 20). Antennal segment III small, about as wide as long (Fig. 8), with no sense cone, IV with 2 stout sense cones, apex of V asymmetric with one short stout sense cone and one small sense cone on inner apex. Pronotum with little reticulation medially but with transverse reticulation on posterior third, all five pairs of major setae capitate. Metanotum weakly reticulate, reticles with few internal markings, bearing 10 small setae (Fig. 26). Fore tarsal tooth large, about as long as tarsal width, hamus also prominent ventrally. Prosternal ferna with anterior margin of mesoeusternum (Fig. 31); metathoracic sternopleural sutures broadly eroded. Pelta broadly triangular, reticulate; tergites II-VII each with only posterior pair of wing-retaining setae; tergite IX setae capitate and shorter than basal width of tube; tube broader in basal than in apical third (Fig. 38).

Measurements (holotype de-alate female in microns). Body length 1700. Head, length 160; width medially 150; po setae 15. Pronotum, length 145; width 250; prothorax width across coxae 350; major setae – am 18, aa 25, ml 12, epim 35, pa 35. Fore wing length ?; sub-basal setae 12, 20, 35. Tergite IX setae S1 50, S2 50. Tube, basal width 65, length 75. Antennal segments III–VIII length 30, 45, 43, 45, 40, 25.

Female microptera. Very similar to macroptera but ocelli slightly smaller; fore wing length 120.

Male microptera. Similar to female but fore tarsal tooth not as large; sternites without transverse bands of specialised reticulation.



FIGURES 28–39. *Adrothrips* prosternites and abdomen. (28) *cotteri*; (29) *latrarei*; (30) *lihongae*; (31) *vernoni*; (32) *akanthus*; (33) *aureus*; (34) *cotteri*; (35) *intermedius*; (36) *mitchelli*; (37) *systenus*; (38) *vernoni*; (39) *westoni*.

Specimens studied. Holotype female de-alate macroptera, **South Australia**, Kangaroo Island, American River, on *Allocasuarina verticillata*, 31.iii.2021 (LAM6477) in ANIC.

Paratypes (female micropterae except where indicated); same site and host as holotype, Kangaroo Island, 4 on

29.xi.2021, 1 on 3.iv.2021; Stokes Bay, 2 on 30.xi.2021; Destrey's Bay Road, *Allocasuarina muelleriana*, 1 female on 1.xii.2021. **New South Wales**, Bermagui, 1 female from dead bark, 20.iii.1991. **Australian Capital Territory**, Canberra, on *A. verticillata*: Mt Stromlo, 4 on 25.xii.2021, 3 on 1.i.2022, 1 male 1 female macroptera on 4.ii.2022; Oakey Hill, 8 females, 2 males, 29.xi.2002; Mt Ainslie, 1 female macroptera, 4 females, 2 males with larvae from woody gall, 11.vi.1995.

Comments. Despite multiple efforts over the past 30 years in the hills around Canberra, only a single gall has ever been found that included a breeding colony of this species. Most available specimens are micropterae and have been obtained only by beating the trees for prolonged periods, with no obvious association with either the green or woody tissues. This species is remarkable for the large fore tarsal tooth (Fig. 20) and the small third antennal segment (Fig. 8). It appears to be closely associated with *A. verticillata*, with only a single female ever taken from a different species.

Adrothrips westoni sp.n.

(Figs 9, 19, 39)

Female microptera. Body and head mainly yellow, anterior margin of head shaded, pronotum and metanotum with pair of brown patches, extending medially on tergites II–IV; tube shaded at apex; femora and tibiae with brown markings; antennal segments IV–VIII brown. Head slightly longer than wide, postocular setae small and capitate; vertex with weak transverse reticulation. Maxillary stylets retracted into eyes (Fig. 19), crossing over near ocelli then re-crossing at occipital ridge, with one flexure before entering the mouth cone. Antennal segment III short with no sense cone (Fig. 9), IV with 2 sense cones, apex of V asymmetric with one short stout sense cone. Pronotum with weak, complicated reticulation, all five pairs of major setae small to minute, weakly capitate or more frequently finely acute. Mesopresterum either absent or fully fused to transverse anterior margin of mesoeusternum. Metanotum weakly reticulate, reticles without internal markings, bearing 10 small setae. Fore wing very small, subbasal setae minute. Fore tarsus with small tooth arising near base. Pelta broadly D-shaped, reticulate; tergites II–VII each with only posterior pair of wing-retaining setae; tergite IX setae capitate and shorter than basal width of tube; tube slightly broader in basal third and narrowing to apex (Fig. 39).

Measurements (holotype female in microns). Body length 1730. Head, length 210; width medially 200; po setae 12. Pronotum, length 135; width 250; prothorax width across coxae 300; major setae – am 5, aa 10, ml 5, epim 12, pa 12. Fore wing length 40. Tergite IX setae S1 30, S2 35. Tube, basal width 75, maximum width 85, length 115. Antennal segments III–VIII length 35, 50, 45, 50, 40, 25.

Male microptera. Similar to female, but tube scarcely wider in basal third; sternites without transverse band of specialised reticulation.

Specimens studied. Holotype female microptera, **South Australia**, Kangaroo Island, American River Village, from *Allocasuarina verticillata*, 8.iv.2022, Alice Wells (LAM6525), in ANIC.

Paratypes: one female collected with holotype; **Australian Capital Territory**, Canberra, Mt. Majura, one female from *A. verticillata*, 24.iv.1995; A.C.T., Canberra, Weston, Oakey Hill, one male from *A. verticillata*, January 2016.

Comments. Despite frequent collecting efforts, only four specimens of this species have been found, at three different localities but all from *A. verticillata*. It shares with *A. akanthus* the reduced number of tergal wing-retaining setae and has similar maxillary stylets. It differs in having antennal segment III short with a narrow pedicel, the mesopresternum absent, the posterior tergites without short stout setae, and the tube of females much less robustly reticulate (Fig. 39).

Akthethrips Mound

Akthethrips Mound, 1970: 452. Type species Akthethrips strobus Mound, by monotypy.

The single species that is placed in this genus is distinguished from other Phlaeothripinae with convoluted maxillary stylets by the prolongation of the head between the basal antennal segments (Fig. 40). This is particularly obvious

in females in which the head is more than 2.5 times as long as wide. However, the head of the available males is much shorter and scarcely 1.5 times as long as wide, and the prolongation is only half as long as the first antennal segment. The presence of one sense cone on antennal segment III and three on IV, also most other character states in the diagnosis, suggest a relationship to the genus *Heligmothrips*, but the more basal position of the sensorium on antennal segment II is unusual.

Diagnosis. Small brown macropterous Phlaeothripinae with prominent interantennal projection in female. Head about twice as long as wide; large female with interantennal projection extending to apex of antennal I, shorter in male; eyes longer on dorsal than ventral surface; postocular setae well developed in large female and male, reduced in small female; mouth cone short and rounded; maxillary stylets elongate, crossing over each other near base of head, with one lateral convolution; mandible small, restricted to mouth cone. Antennae 8-segmented; segment II with campaniform sensillum placed medially or toward the base; segment III with 1 sense cone, IV with 3 (or 2) sense cones; VIII distinct from VII but not constricted at base. Pronotum narrower than prothorax (Fig. 41), all 5 pairs of major setae present; notopleural sutures complete. Prosternal basantra absent; mesopresternum reduced to two triangles; metathoracic sternopleural sutures long. Mesonotal midlateral setae well developed with apices expanded; metanotum reticulate medially with 1 pair of small fine setae. Fore tarsal tooth larger in female than in male. Fore wing parallel-sided, duplicated cilia present, 3 sub-basal setae present with expanded apices. Pelta elongate triangular (Fig. 42); tergites II–VII with 2 pairs of sigmoid wing-retaining setae arising laterally; tube short with long anal setae; sternites with transverse row of about 10 discal setae; male sternite VIII with no pore plate.

Akthethrips strobus Mound

(Figs 40, 41, 42)

Akthethrips strobus Mound, 1970: 452.

Based on two females and one male taken at Moree, this species is known otherwise only from both sexes take more recently in South Australia. The maxillary stylets are parallel to each other and close together, but cross over each other at the base of the head and each produces two large loops. Tergite VIII of females has a group of short stout discal setae. The male listed below collected at Iron Baron together with three females differs from the male collected at a site nearby and also from the original paratype in the following character states: mesopresternum and anterior margin of the mesoeusternum heavily eroded; fore legs stouter with larger fore tarsal tooth; antennae shorter; fore wings shorter than in macropterae. This specimen is either a different species or possibly an unusual major form of *strobus*.

Specimens studied. New South Wales, Moree 50km north, holotype female from *Casuarina glauca*, 16.vii.1968, in ANIC. South Australia, Whyalla, Iron Baron, 3 females and 1 male from *Casuarina pauper*, 12.vi.1997; Whyalla, Middleback Station, 1 male from *Casuarina pauper*, 14.iii.1997.

Enigmathrips gen.n.

Type species Enigmathrips carnarvoni sp.n.

Diagnosis. Macropterous or micropterous Phlaeothripinae with convoluted maxillary stylets and elongate pronotum. Antennae 8-segmented (Fig. 43), II with sensorium on basal half of segment, III with one short sense cone, IV with 3 short sense cones; VII pedicillate, VIII small. Head almost twice as long as wide (Fig. 44), posterior margin eroded medially; ocelli small, posterior pair wide apart close to eyes; maxillary stylets retracted to eyes, crossing over each other near eyes but then wide apart and with complex flexures posterolaterally before entering long and pointed mouth cone. Pronotum much narrower than prothorax (Fig. 46), anterior margin strongly eroded between weak anteromarginal setae; remaining setae long and pointed, epimera with second seta well developed; notopleural sutures complete. Prosternal basantra absent; ferna large and wide apart; mesopresternum reduced to small median sclerite (Fig. 45); metathoracic sternopleural sutures long. Meso and metanota weakly sculptured, metanotum with one or more pairs of minor setae medially in addition to small pointed median pair. Fore tarsal tooth stout, longer than tarsal width. Fore wing broad, parallel sided, with closely ciliate margins but without duplicated

cilia; with two long weakly capitate sub-basal setae. Pelta triangular with apex truncate; tergite II lateral margins eroded; II–VII with anterior pair of wing-retaining setae absent, only II–IV with posterior pair and these weakly curved; II–VII each with median transverse irregular row of about 20 setae; tergal posterolateral setae long and weakly capitate, but on IX shorter than tube; tube shorter than head.

Comments. The structure of the single species for which this genus is erected is remarkable and the generic relationships are difficult to interpret. The structure of the antennae is typical of species in the *Liothrips*-lineage, in the number and size of the sense cones on segments III and IV, and the short segment VIII that is broadly joined to segment VII. In contrast, the following character states are more typical of the Plectrothripini: antennal segment II sensorium on basal half of segment, pronotum elongate and narrow, tergite II eroded laterally. A particularly unusual feature is that despite the presence of broad, parallel-sided fore wings there are no sigmoid wing retaining-setae on any of the tergites.

Enigmathrips carnarvoni sp.n.

(Figs 43, 44, 45, 46)

Female macroptera. Body light brown, anterior margin of head and anterior margins of tergites darker; all setae pale; legs mainly yellow; antennal segment I brown, II–VIII yellow with light shadings; fore wing uniformly shaded with apex and extreme base paler. With the generic character states given above.

Measurements (holotype female in microns). Body length 3010. Head, length 300; width medially 175; po setae 105. Pronotum, length 350; width 300; prothorax width across coxae 550; major setae – am 50, aa 120, ml 115, epim 130, pa 125. Fore wing length 1450; width 120; sub-basal setae 100. Tergite V posterolateral setae 180; setae S1 on tergite IX 130. Tube, basal width 115; length 250. Antennal segments III–VIII length 100, 85, 85, 75, 75, 30.

Female microptera. Very similar to macroptera in size and structure; fore wing lobe less than 200 microns long.

Specimens studied. Holotype female macroptera, **Queensland**, Carnarvon Station, by barkspray on *Acacia harpophylla*, 13.x.2014 (DJTree 1956), in ANIC.

Paratypes: one female microptera collected with holotype, one female similarly collected on same date nearby at Piebald Spring Road; Lake Nuga Nuga [40km East of type locality], 2 female micropterae by barkspray on *Acacia harpophylla*, 8.vi.2014 (in QDPC and ANIC).

Heligmothrips Mound

Heligmothrips Mound, 1970: 453. Types species Trichothrips erinaceus Karny

This genus of dark brown, usually macropterous species of Phlaeothripinae, is a member of the *Liothrips* lineage, and is presumably derived from the complex of taxa associated with the genus *Teuchothrips*. Members of the latter genus do not usually have the maxillary stylets elongate and crossing over in the head, although two species with this condition are known from New Caledonia, both of which are associated with leaf distortion on species of *Hibbertia* [Dilleniaceae] (Mound & Goldarazena 2022). Moreover, some specimens here identified as *H. brevidens* from Kangaroo Island, also *H. narrabri* **sp.n.** and H. *xanthoskelus* **sp.n.**, have the stylets parallel in the middle of the head (Figs 51–59). Study of species in this genus is technically difficult, because in order to study the convoluted maxillary stylets specimens must be partially bleached without disrupting the position of these stylets. In some species between specimens in colour of antennae, pronotal setae and fore wings are particularly difficult to assess. Moreover, the precise orientation of the maxillary stylets within the head is possibly not as consistent between species as indicated in Mound (1970), and the names *H. erinaceus* and *H. gracilior* (couplet 7 in key below) possibly involve a complex of species. Far more field work would be needed to establish if the observed differences are consistent, and if they are associated with different host plants, localities or seasons.

Diagnosis. Dark brown, usually macropterous Phlaeothripinae, body surface more or less reticulate. Head

about as long as wide, maxillary stylets retracted to eyes and usually crossing over each other in middle of head, and each with a simple or complex loop or convolution posteromedially; mouth cone acute; postocular setae with expanded apices. Antennae 8-segmented; VII and VIII broadly joined; III with 1 sense cone, IV with 3 sense cones (2 in *eiletus* and *narrabri*). Pronotum with 5 pairs of major setae; notopleural sutures complete. Prosternal basantra absent, ferna widely separated; mesopresternum varied, complete or with two triangles weakly joined or absent medially; sternopleural sutures long. Fore tarsus with a tooth in both sexes; fore femur enlarged in major individuals. Mesonotal lateral setae capitate, metanotal median setae usually acute. Fore wing broad and closely ciliate; duplicated cilia present (absent in *narrabri*); 3 sub-basal setae present. Tergites II–VII each with 2 pairs of wing-retaining setae; tergite IX setae S1 and S2 long and capitate. Male sternite VIII with large pore plate.

Key to *Heligmothrips* species

1. 	Maxillary stylets closely parallel medially or crossing over each other, only one simple flexure posterolaterally (Figs 51, 58) 2 Maxillary stylets crossing over each other medially (rarely parallel), with one or more complex loops or coils posterolaterally (Figs 52–56)
2. 	Head elongate, at least 1.5 times as long as wide (Fig. 57); pronotum about as long as wide and not extending fully across prothorax (Fig. 68)
3. 	Metanotal reticles large and weak, each with a spot medially (Fig. 61); antennal segments IV–V uniformly brown, each with 2 sense cones; fore wings without duplicated cilia, or micropterous
4. 	Mesopresternum divided into two lateral triangles or weakly connected medially; pronotal anteromarginal setae sometimes short but as broadly capitate as remaining 4 pairs of major setae (Fig. 51); pronotal anteroangular setae of male no more than 1.5 times as long as those of female; fore wing with 12 or more duplicated cilia;
5. 	Maxillary stylets arranged posterolaterally into pair of regular coils (Fig. 54); metanotal median setae stout, capitate and half as long as metanotum (Fig. 60); antennal segment IV with 2 sense cones; only micropterae known
6. 	Head longer than wide (Fig. 56), pronotum slender but slightly wider than long, narrower than prothorax width; body colour light brown with weak sculpture
7. -	All femora and tibiae yellow or brownish yellow xanthoskelus sp.n. All femora dark brown, also mid and hind tibiae 8
8 	Pronotal major setae dark brown; maxillary stylets cross over each other in head at level of postocular setae, then often re-cross through a sharp angle at base of head, before producing two broad curves laterally (Fig. 52)

Heligmothrips brevidens (Hood)

(Fig. 51)

Liothrips brevidens Hood, 1918: 137 *Teuchothrips spinosus* Moulton, 1968: 102. *Cryptothrips reticulaticeps* Girault, 1927b: 1 **syn.n.**

Described from three females and four males taken by sweeping vegetation near Charters Towers in northern

Queensland in 1912/13. The synonym, *spinosus* was described from one female taken near Newcastle in New South Wales and one male from Bribie Island, in southeastern Queensland. The single female from which Girault described *reticulaticeps* was collected in southeastern Queensland from mangrove at Banyo, Brisbane. This species was transferred to the genus *Heligmothrips* by Mound (1974: 40), but with no comment or details other than that the species was a member of the Phlaeothripinae not Idolothripinae. The maxillary stylets of the specimen do not cross over each other but are close together medially. However, a similar arrangement of the stylets has been seen in a few specimens of *brevidens* from *Allocasuarina muelleriana* on Kangaroo Island. The fore wing of the reticulaticeps holotype bears only three duplicated cilia, whereas in most specimens identified as *brevidens* there are between 9 and 15 duplicated cilia. Unfortunately, the *reticulaticeps* specimen is too contracted to observe the mesopresternum.

The maxillary stylets of *H. brevidens* cross over each other at the level of the postocular setae. They then recross at the posterior margin of the head, with the single posterolateral flexure usually involving no more than a single sharp turn close to the lateral margins of the mouth cone (Fig. 51). There is considerable variation in body size among individuals, with females varying in body length within any single population from less than 2mm to more than 3mm. Males are equally variable in body length but are generally smaller. However, large males commonly have the pronotal anteroangular setae twice as long as the anteromarginals (much longer than in females), and the largest male studied has the anteromarginal setae scarcely larger than the pronotal discal setae. In females the pronotal setal pairs are smaller and remain almost co-equal in length regardless of body size.

The colour of the pronotal setae is usually light brown, but these setae are pale in a few specimens, and dark brown in a few others. The common form around Canberra is similar to the *brevidens* holotype, with the basal half of antennal segments IV–V largely yellow and the pronotal setae shaded. But in the series from Kangaroo Island the antennae are largely brown and the pronotal setae varying from weakly shaded to pale. The fore wing also varies among populations in the extent of brown shading, despite having been considered "pale" by Hood. Despite these variations, the specimens listed below are all considered likely to represent the same species, although the three specimens from Timor Leste are particularly unusual with slender, dark pronotal setae.

Specimens studied. **Australian Capital Territory**: Casuarina Sands, from *C. cunninghamiana*, 2 females, 1 male, 6.iv.1968; 3 females, 2 males, 23.x.1994; 4 females, 4 males, 10.xi.2002. **New South Wales**: near Taralga, 1 female, 1 male from *C. cunninghamiana*, 2.iv.1968; Warrumbungle N.P., 3 females from *Casuarina*, 13.iii.2008. **Victoria**: near Mallacoota, 3 females 3 males from *Allocasuarina paludosa*, 29.xii.2004. **Tasmania**: Lake Pedder, 1 male, 24.ii.2004. **South Australia**: Kangaroo Island, 6 females 5 males from *A. muelleriana*, 1.xii.2021; Ngarkat Park, 1 female from dead wood, 4.x.2013. **Queensland**: near Charters Towers, 3 males from *Casuarina*, 3.vii.1995; Hughenden, 66km north, 2 females, 1 male from *Casuarina*, 14.x.2015; Carnarvon Station, 1 female from *Casuarina cunninghamiana*, 11.x.2014; Brisbane, The Gap, 2 females from *Casuarina*, 30.xii.2006; Brisbane, Banyo, holotype female of *reticulaticeps*. **Western Australia**: Barrow Island, 3 females, 1 male, iv/v.2005. **Timor Leste**: Aileu, 2 females, 1 male from *Casuarina*, 22.viii.2018.

Heligmothrips eiletus Mound

(Figs 54, 55, 60)

Heligmothrips eiletus Mound, 1970: 458

This unusual species was described from a single micropterous male but has subsequently been found to be more widespread. Unlike any of the other known *Heligmothrips* species, the maxillary stylets are arranged into two discrete but irregular coils (Fig. 54). The stylets of the larva are more irregularly convoluted (Fig. 55). The species is also unusual in having only two sense cones on antennal segment IV, and a stout pair of capitate setae medially on the metanotum (Fig. 60). Despite being found at several localities, no winged specimens have been collected.

Specimens studied. All micropterae. Holotype male, **New South Wales**: Moree 45km north, from *Casuarina glauca*, 16.vii.1968. **Victoria**: Mildura Botanic Gardens, 6 females, 8 males with larvae on *C. obesa*, 13.iv.2022; **New South Wales**: Balranald 20km west, 1 male with larvae on *C. obesa*, 14.iv.2022; Moree 40km north, 4 females, 7 males on *C. cristata*, 20.v.2022.



FIGURES 40–50. Akthethrips, Enigmathrips, Phallothrips, Thaumatothrips. A. strobus 40-42: (40) head; (41) pronotum; (42) metanotum & pelta. E. carnarvoni 43–46: (43) antenna; (44) head; (45) prosternites; (46) pronotum. (47) T. froggatti head & fore legs. P. houstoni 48–50: (48) microptera; (49) macroptera; (50) macroptera tergites V–VII.

Heligmothrips erinaceus (Karny)

(Fig. 52)

Trichothrips erinaceus Karny, 1920: 41; 1924: 26 (Figs 32–33). *Teuchothrips fuscipennis* Moulton, 1968: 100.

Karny described this species from a single female taken at Cedar Creek, Queensland, a locality within the Mt

Tamborine Park just south of Brisbane. The five-line description gave no useful details, and his completed account in 1924 of the Thysanoptera from the Mjoberg expedition to Australia provided images of the whole body and antenna but no description. The unique specimen was subsequently slide-mounted but is in a seriously damaged condition. Moulton described *fuscipennis* from the holotype female taken at Liverpool (Sydney) in New South Wales, and three paratype females from Bribie Island, Queensland. The holotypes of both species were restudied and described by Mound (1970), who compared them to specimens taken from various sites in eastern Queensland and New South Wales. Antennal segment III is relatively slender and mainly yellow, but the pronotal setae are strongly shaded. In males the anteroangular pronotal setae are much longer than in females. The maxillary stylets cross over each other usually anterior to the postocular setae. They re-cross each other at the posterior of the head often through a sharp right-angle, before producing a complex set of loops posterolaterally (Fig. 52). However, in most character states *erinaceus* is very similar to *gracilior*, a species that is distinguished only by the pale pronotal setae and the maxillary stylets arranged more irregularly into large loops.

Specimens studied. **Australian Capital Territory**: Mt Majora, 2 small males from *Allocasuarina verticillata*, 24.iv.1995. **New South Wales**: Batemans Bay, from *Casuarina glauca*, 1 male, 16.ii.1961; 4 females, 6 males, 20.xi.1994; 6 females, 6 males, 7.xii.1996; 7 females, 5 males, 1.vi.2022; Tarago 20km East, 2 females on *A. littoralis*, 11.ix.2021; Gosford, 1 female form *Casuarina*, 20.xi.1994; Pottsville, 2 females from *C. glauca*, 3.ix.2009. **Queensland**: Mt Malloy 25km north, 4 females, 6 males from *Casuarina*, 6.vii.1995; Atherton 10km north, 3.v.1964; Carnarvon Station, Blue Water Springs, 3 females from *Casuarina*, 9.x.2014; Brisbane, The Gap, from *Casuarina*, 1 male, 30.xii.2006, 3 females, 30.x.2007; Mt Glorious 15km west, Red Cedar Park, 3 females from *C. equisetifolia*, 20.ix.2009. **South Australia**: Kangaroo Island, Stokes Bay, 1 female from *Allocasuarina verticillata*, 30.xi.2021.

Heligmothrips exallus sp.n.

(Figs 56, 62, 64, 67)

Female macroptera. Body light brown, head paler posteromedially, tube dark brown; antennal segment II paler at apex, III paler basally, IV–VIII uniformly brown; all tibiae paler than brown femora, tarsi yellow; male setae pale; fore wings very weakly shaded. With the character states given in the generic diagnosis, except as follows: head longer than wide (Fig. 56), vertex with little or no sculpture, genae without prominent setae; postocular setae capitate, extending to hind margin of eyes; eyes smaller ventrally than dorsally; hind ocelli close to eyes; maxillary stylets cross over at level of eyes, then re-cross through very sharp angle at posterior margin of head before producing one large circle posterolaterally and entering mouth cone; mouth cone long and pointed. Antennal segments not elongate, III less than twice as long as wide with basal stem bearing small irregular rings (Fig. 67). Pronotum elongate, only slightly wider than long but much narrower than prothorax (Fig. 56); major setae long, pale and capitate. Mesonotal lateral setae capitate. Metanotum very weakly reticulate, median setae finely pointed (Fig. 62). Prosternal ferna very wide apart, mesopresternum of two lateral triangles only weakly linked medially (Fig. 64). Fore tarsal tooth almost as long as tarsal width. Fore wing with 8 duplicated cilia. Pelta elongate bell-shaped (Fig. 62); tergites II–VII each with 2 pairs of wing-retaining setae of which the anterior pair is small on each tergite; tergite IX setae long and capitate; tube shorter than head.

Measurements. Body length 2100. Head, length 175; width medially 140; po setae 40. Pronotum, length 200; width 230; prothorax width 300; major setae – am 25, aa 50, ml 45, epim 70, pa 30. Fore wing length 700; sub-basal setae 35. Tergite IX setae S1 105, S2 95. Tube, basal width 75, length 135. Antennal segments III–VIII length 55, 48, 50, 45, 45, 25.

Specimens studied. Holotype female macroptera, **Queensland**, Carnarvon Station, from woodland barkspray, 16.x.2014.

Comments. This species shares many character states with other species in the genus *Heligmothrips*, but it is clearly aberrant within the genus in its more elongate shape, relatively short antennae and weakly sculptured surface.



FIGURES 51–59. Heligmothrips species heads and stylets. (51) brevidens; (52) erinaceus; (53) gracilior; (54) eiletus; (55) eiletus larva; (56) exallus; (57) macropus; (58) narrabri; (59) xantoskelus.

Heligmothrips frickeri Mound

Heligmothrips frickeri Mound, 1970: 460

Described from a single female taken in northern Australia, the specimens listed below all share the same character states of a fully transverse mesopresternum, very small pronotal anteromarginal setae, and very few fore wing duplicated cilia. In other features these specimens are very similar to those identified as *H. brevidens*, and it is possible that they represent no more than aberrant specimens of that species.

Specimens studied. Holotype female, **Northern Territory:** McArthur River, 18.vii.1961. **Northern Territory:** Gregory N.P., Bullita Outstation, 1 female, 2 males, 3.vii.1986. **Western Australia**: Dampier 90km southeast, 2 females, 2 males, ix.1995. **South Australia**: Kangaroo Island, 1 female, 26.xii.2002.

Heligmothrips gracilior (Hood)

(Fig. 53)

Liothrips gracilior Hood, 1918: 136 *Teuchothrips albipennis* Moulton, 1968: 99.

This species was described from a single female collected from *Casuarina* species at Pentland in northern Queensland. The junior synonym, *albipennis* was described from several specimens, with the holotype female taken from *Casuarina* at Ivanhoe, New South Wales and paratypes from arid areas in northern South Australia. Judging from the specimens listed below this species seems to be associated particularly with *Casuarina* species in the arid zone across Australia. It is the only species in the genus with the pronotal major setae long but pale and colourless. As in the other species, males usually have the pronotal anteroangular setae longer than females, but the slender triangles forming the mesopresternum are sometimes narrowly complete medially. As indicated above, it is closely similar to *erinaceus* in colour and structure, apart from the pale pronotal setae and the maxillary stylets usually arranged into larger convoluted circles posterolaterally (Fig. 53).

Specimens studied. **Queensland**: Charters Towers 200km north, 1 female from *Casuarina*, 3.vii.1995; Carnarvon Gorge, 1 male from Casuarina, 11.v.2017; Bowen, 1 female, 25.iii.1998; Dalby, Broadwater Lake, from *Casuarina cristata* foliage,1 female, 1 male, 8.iii.2008, 1 male, 27.ii.2003. **Victoria**: Mildura 50km west, 2 males from *C. pauper*, 25.iv.1995; Mildura 30km south, 2 females 1 male from *A. luehmanni*, 4.xii.2021. **South Australia**: Renmark 80km northwest, 5 females 4 males in traps, iii–v.1995; Whyalla district, 10 females, 5 males from *Casuarina pauper*, iii–vi.1997. **Western Australia**: from *C. obesa*: Murchison River Crossing, 6 females 3 males, 25.iv.1997 and 12.x.2003; Northampton 60km east, 2 females, 5 males, 25.iv.1997. Perth, Gingin, 1 male from grasses, 29.ix.1995.

Heligmothrips macropus sp.n.

(Figs 57, 68)

Female macroptera. Body dark brown, fore tibiae and all tarsi paler; antennae brown, apex of II paler and III brownish yellow; major setae pale to very weakly shaded; fore wings pale. With the character states given in the generic diagnosis, except as follows: head longer than wide, genae without prominent setae (Fig. 57); postocular setae capitate, extending well beyond hind margin of eyes; eyes smaller ventrally than dorsally; hind ocelli close to eyes; maxillary stylets cross over at level of postocular setae, the re-cross at posterior margin of head and producing one simple posterolateral flexure before entering mouth cone; mouth cone bluntly pointed. Antennal segments not elongate, III about twice as long as wide. Prothorax large, pronotum elongate, slightly longer than wide and much narrower than prothorax (Fig. 68); reticulate on anterior third, also laterally; anteromarginal setae minute, remaining major setae long, pale and capitate. Mesonotal lateral setae capitate. Metanotum reticulate, median setae finely pointed. Prosternal ferna large, mesopresternum of two lateral triangles, mesoeusternum anterior margin convex. Fore tarsal tooth massive, almost as long as tarsal width. Fore wing with 13 duplicated cilia. Pelta elongate bell-shaped; tergites II–VII each with 2 pairs of wing-retaining setae of which the anterior pair is small on each tergite; tergite IX with all 3 major setae long and capitate; tube broad at base, shorter than head.

Measurements. Body length 2400. Head, length 230; width medially 145; po setae 80. Pronotum, length 300; width 300; prothorax width 400; major setae – am 5, aa 75, ml 60, epim 75, pa 50. Fore wing length 850; sub-basal setae 50. Tergite IX setae S1 155, S2 115. Tube, basal width 100, length 180. Antennal segments III–VIII length 70, 68, 55, 55, 55, 30.

Specimens studied. Holotype female, **South Australia**: Kangaroo Island, Stokes Bay, from *A. verticillata*, 30.xi.2021 (LAM6501).

Paratypes, **South Australia**: 2 females taken with holotype.

Comments. Known only from Kangaroo Island, hence the specific epithet, this species is remarkable amongst members of the *Teuchothrips* group for the elongate head with parallel genae. The pronotum resembles that of *H. exallus* **sp.n**. in being unusually long, about as long as wide and much narrower than the prothorax. However, the arrangement of the maxillary stylets is similar to that found in *H. brevidens* in having only a single lateral flexure.

Heligmothrips narrabri sp.n.

(Figs 58, 61, 66)

Female macroptera. Body, legs and antennae brown, tarsi and basal stem of antennal segment III yellowish brown; major setae pale, fore wing very weakly shaded. With the character states given in the generic diagnosis, except as follows: head slightly wider than long, genae without prominent setae; postocular setae capitate, extending to hind margin of eyes; eyes smaller ventrally than dorsally; hind ocelli close to eyes; maxillary stylets retracted almost to eyes but not crossing over each other (Fig. 58), with one simple flexure before entering mouth cone; mouth cone pointed and extending across prosternal ferna. Antennal segments not elongate, III about twice as long as wide with one sense cone small, IV with 2 sense cones. Pronotum transverse, with weak sculpture medially (Fig. 58); major setae short, pale and capitate. Mesonotal lateral setae capitate. Metanotum fully but not strongly reticulate, each reticle with a small median dot; median setae finely pointed (Fig. 61). Prosternal ferna slender and transverse; mesopresternum complete but slender, mesoeusternum anterior margin straight (Fig. 66). Fore tarsal tooth small. Fore wing without duplicated cilia. Pelta broadly triangular, apex truncate (Fig. 61); tergites II–VII each with 2 pairs of wing-retaining setae of which the anterior pair is small on each tergite, both pairs reduced on II and VII; tergite IX with all 3 major setae long and capitate; tube shorter than head.

Measurements. Body length 1550. Head, length 150; width medially 155; po setae 20. Pronotum, length 125; width 220; major setae – am 20, aa 25, ml 20, epim 20, pa 25. Fore wing length 600; sub-basal setae 20. Tergite IX setae S1 60, S2 60. Tube, basal width 60, length 110. Antennal segments III–VIII length 45, 30, 45, 50, 50, 25. *Female microptera*. Similar to macroptera but metanotum more transverse; fore wing lobes less than one-third of thorax width; pelta broader; tergal wing-retaining setae reduced.

Specimens studied. Holotype female macroptera, New South Wales: Narrabri 27km South, from *Allocasuarina luehmannii*, 21.v.2022 (Alice Wells) (LAM 6550).

Paratype New South Wales: 1 macroptera, 4 micropterae females, taken with holotype.

Comments. This is a distinctive species with a small marking between each metanotal reticle and fore wings without duplicated cilia. The condition of the maxillary stylets not crossing over each other is not unique within this genus, because it is also reported above for some individuals of *brevidens* as well as for the species below.

Heligmothrips xanthoskelus sp.n.

(Figs 59, 63, 65)

Female macroptera. Body uniformly brown, tube darkest; all legs much paler, variably yellow to light brown with fore femora darkest; apex of antennal segment II and all of segment III almost yellow, IV–VIII brown with basal third of IV and V paler; major setae shaded but not dark; fore wing pale with base brown. With the character states given in the generic diagnosis, except as follows: head slightly wider than long, genae without prominent setae; postocular setae capitate, extending slightly beyond hind margin of eyes; eyes smaller ventrally than dorsally; hind ocelli not close to eyes; maxillary stylets retracted to eyes (Fig. 59), not crossing over each other, but at level of base of head twisting sharply laterally into figure-of-eight convolutions before entering mouth cone; mouth cone pointed

but not extending to prosternal ferna (Fig. 65). Antennal segment III longer than wide, IV with 3 sense cones, V and VI each with ventrolateral apex slightly prolonged. Pronotum transverse, with extensive reticulate sculpture (Fig. 59); major setae short, capitate and weakly shaded. Mesonotal lateral setae capitate. Metanotum strongly reticulate; median setae small and finely pointed (Fig. 63). Prosternal ferna transverse; mesopresternum complete but narrowed medially (Fig. 65). Fore tarsal tooth small. Fore wing with about 8 duplicated cilia. Pelta quadrate with apex truncate (Fig. 63); tergites II–VII each with 2 pairs of wing-retaining setae of which anterior pair on each tergite is small; tergite IX with all 3 major setae long and capitate; tube shorter than head.



FIGURES 60–68. *Heligmothrips* species thorax and antenna. (60) *eiletus*; (61) *narrabri*; (62) *exallus*; (63) *xanthoskelus*; (64) *exallus*; (65) *xanthoskelus*; (66) *narrabri*; (67) *exallus* antenna; (68) *macropus* pronotum.

Measurements. Body length 2100. Head, length 200; width medially 220; po setae 35. Pronotum, length 160; width 330; major setae – am 35, aa 35, ml 30, epim 45, pa 35. Fore wing length 750; sub-basal setae 35. Tergite IX setae S1 70, S2 50. Tube, basal width 85, length 160. Antennal segments III–VIII length 70, 70, 60, 50, 45, 25.

Male macroptera. Very similar to females but with legs slightly more shaded; largest male with fore femora enlarged, fore tarsal claw about 0.5 as long as tarsal width, and fore tibia with small tubercle at inner apex, smaller males with more slender fore legs. Tergite IX setae S2 slightly shorter than S1; sternite VIII with small circular pore plate medially.

Specimens studied. Holotype female macroptera, **New South Wales**: Moree 40km north, from *Casuarina cristata*, 20.v.2022 (Alice Wells) (LAM6548).

Paratypes: New South Wales: 2 females, 3 males taken with holotype.

Comments. The pale legs contrasting with the dark body of this species were noted when it was taken alive together with the dark brown micropterous species, *H. eiletus*. The maxillary stylets are also distinctive in forming two large rings in a figure-of-eight, and the truncate apex to the pelta is also unusual for species in this genus. The male is unique in the genus for having a small, circular pore plate on sternite VIII.

Iotatubothrips Mound & Crespi

Iotatubothrips Mound & Crespi, 1992: 400. Type species Iotatubothrips crozieri Mound & Crespi, by monotypy.

The two species previously described in this genus, plus the new species described below, are all known to induce woody galls on the stems of *Casuarina* species. Within these galls the species develop large colonies, mainly of micropterous females with relatively few males and even fewer macropterae. The majority of character states observed on these species are subject to extreme reduction. Many body parts are particularly weakly sclerotised, such that it is difficult to recognise relationships to any other genera. Moreover, each of the species has proved difficult to slide-mount, because the body contents are remarkably resistant to chemical treatment. Curiously, the abdomen of females lacks a fustis, the sclerotised rod in segment IX that is usually found in Phlaeothripidae. However, this genus shares more character states with *Adrothrips* than with any other Phlaeothripinae genus. The structural variation between morphs and its relationship to aspects of the biology of two species was discussed by Mound *et al.* (1998), together with illustrations of the differences between macropterae and micropterae in setae on the head and pronotum.

Diagnosis. Small, light brown, usually micropterous Phlaeothripinae in woody galls on *Casuarina* species. Head slightly wider than long; postocular setae short (long in macropterae); maxillary stylets retracted almost to postocular setae, less than one-third of head width apart. Antennae 8-segmented; segments short and wide, III without sense cones, IV with 2 sense cones. Pronotum transverse, with 5 pairs of major setae, these long and slender in macropterae. Prosternal basantra absent; ferna irregular; mesopresternum reduced to lateral triangles that are often fused to mesoeusternal margin; metathoracic sternopleural sutures present but irregular. Metanotum weakly reticulate, with several pairs of small setae medially. Fore tarsal tooth prominent in both sexes; fore tibia with or without tubercle on inner apex. Fore wing broad, without duplicated cilia. Pelta bell-shaped in macropterae, eroded to small sclerite in micropterae; tergites II–VII each with one pair of wing-retaining setae; tergal lateral setae long and slender; segment IX of female without obvious fustis; tube very short, often much shorter than head; in female dorsal apical margin prolonged beyond ventral margin; in male deeply excavate ventrally to about 90% of length in some species. Male without sternal pore plate; phallotheca slender and unusually long, 5 times as long as basal width in micropterae.

Key to Iotatubothrips species

2.	Fore tibiae of all morphs with no tubercle at inner apex; male macroptera with phallotheca no more than 6 times as long as
	phallobasecrozieri
	Fore tibia inner apex of all females, also male micropterae, with small sharply pointed tubercle; male macroptera without fore
	tibial tubercle; phallotheca about 10 times as long as phallobasekranzae

Iotatubothrips crozieri Mound & Crespi

Iotatubothrips crozieri Mound & Crespi, 1992: 403.

Described from *Casuarina cristata* in northern New South Wales at Walgett and at Warren, this species has been seen from the same tree species in southern Queensland, at Barakula, Dalby, and Goondiwindi, as well as in South Australia near Whyalla on *Casuarina pauper*.

Iotatubothrips kranzae Mound, Crespi & Tucker

Iotatubothrips kranzae Mound, Crespi & Tucker 1998: 11.

This species is known only from Western Australia, Murchison River crossing, where it was found inducing woody galls on stems of *Casuarina obesa*. It represents the only known example of genitalic dimorphism among Thysanoptera, in that the phallotheca of winged males is almost 50% longer than the phallotheca of wingless males.

Iotatubothrips daguilari sp.n.

(Figs 69-73)

Male microptera. Body, legs and antennae brown, tibae, tarsi and antennal segment III paler; major setae hyaline. Head wider than long; vertex with irregular transverse reticulation; postocular setae short and pointed; ocelli very small; maxillary stylets retracted almost to postocular setae, one fifth of head width apart, with maxillary bridge (Fig. 69). Antennae 8-segmented (Fig. 72), III as wide as long without sense cone, IV and V each with 2 stout sense cones placed ventrally, VI with one sense cone, VII narrowed to base. Pronotum transverse, without sculpture lines medially, with five pairs of capitate major setae. Mesonotum with narrowly spaced transverse reticulation, lateral setae small and capitate. Metanotum transverse (Fig. 70), weakly reticulate, median setae short and pointed. Mesopresternum reduced to scattered small fragments; mesoeusternum anterior margin transverse; metathoracic sternopleural sutures short and often incomplete. Fore tarsus with tooth about 0.5 as long as tarsal width; fore tibia ventro-lateral inner apex with small tooth. Fore wing lobe less than 0.3 as long as pterothorax width, without subbasal setae. Pelta reduced to small irregular triangular sclerite (Fig. 70); tergites II–VII each with one pair of widely spaced almost straight or weakly sigmoid wing-retaining setae; tergite IX setae S2 not shorter than S1; tube slightly longer than head (Fig. 71, excavate ventrally for at least half its length. Sternites without pore plates.

Measurements (holotype male in microns). Body length 2200. Head, length 160; width medially 185; po setae 15. Pronotum, length 175; width 300; major setae – am 35, aa 35, ml 60, epim 60, pa 60. Fore wing lobe 130. Tergite IX setae S1 85, S2 110. Tube, basal width 100, length 180. Antennal segments III–VIII length 30, 35, 35, 35, 38, 15.

Female microptera. Closely similar to male in colour and structure, but slightly larger; tube with dorsal apical margin prolonged over ventral margin.

Female macroptera. Similar in colour and structure to micropterae, but ocelli well developed and metanotum more elongate; fore wing widened distally, without duplicated cilia, with (or without) one short capitate sub-basal seta; tergal wing-retaining setae almost straight (Fig. 73).

Specimens studied. Holotype male microptera, **Queensland**, 15km west of Mt Glorious, from woody gall on "Casuarina" twig, 3.x.1999 (LAM 3752) in ANIC.

Paratypes: 6 micropterous males, 30 micropterous females, 4 macropterous females taken with holotype; same locality, from gall on *C. cunninghamiana*, 5 micropterous males, 15 micropterous females, 19.iii.2002.

Comments. This species differs from the two previously described species in the genus in having the pronotal major setae of the micropterae as short and capitate as those of the macropterae. In contrast, in *crozieri* and *kranzae* the pronotal setae of micropterae are long and acute. The macropterae of *crozieri* also usually have the pronotal setae long and pointed, whereas macropterae of *kranzae* and *daguilari* have these setae capitate although distinctly longer in *kranzae* than in the new species. Unfortunately, the host association of this species remains doubtful, because plant samples were not retained for either of the two samples collected. When the second sample was found, the tree involved was growing near a stream and was assumed to be *C. cunninghamiana*, but no similar galls have ever been found anywhere else on this tree species that is widely distributed in eastern Australia.



FIGURES 69–78. *lotatubothrips & Xyelethrips. I. daguilari* 69–73: (69) head & pronotum; (70) metanotum & pelta; (71) tergites IX–X; (72) antenna; (73) macroptera tergites IV–VI. *X. quadritibia* 74–78: (74) prosternites; (75) head; (76) tergites VIII–X; (77) antenna; (78) metanotum & pelta.

Phallothrips Mound & Crespi

Phallothrips Mound & Crespi, 1992: 403. Type species Phallothrips houstoni Mound & Crespi, by monotypy.

The single species recognised in this genus is remarkable for having the difference between winged and wingless adults greater than is known in any other species of Phlaeothripidae (see Mound *et al.* 1998). It lives as a phytophagous kleptoparasite, invading the woody galls created by *Iotatubothrips* species. Colonies have been found on both *C. cristata* in eastern Australia and *C. obesa* in Western Australia. The body structure is so unusual that generic relationships are particularly difficult to suggest, but it seems likely to be a highly aberrant form from within the *Liothrips*-lineage.

Diagnosis. Medium-sized, dark, apterous or macropterous Phlaeothripinae. *Aptera*: Varying greatly in body size (2000–3500 microns body length); head with no ocelli, genae swollen behind small eyes and without setae; postocular setae small; maxillary stylets close together medially; maxillary guides stout and curved, meeting at anterior. Antennae 8-segmented; segment III with one sense cone, IV with 2 sense cones. Pronotum massive, reticulate, major setae short. Prosternal basantra absent; ferna large and transverse; prosternal chitinous islets very large; mesopresternum absent; metathoracic sternopleural sutures present. Mesonotum transverse; metanotum transverse, strongly reticulate with one pair of median setae. Fore tarsal tooth massive; fore femora swollen but without tubercles. Pelta eroded to small circular sclerite; tergal median setal pair long and wide apart; II–VII each with one pair of almost straight wing-retaining setae; tergites VIII and IX of large individuals with many small fine discal setae medially; female segment IX with fustis weakly developed; tube short and conical, with many short setae dorsally and ventrally; anal setae short and stout. Male with phallotheca massive, segment IX enlarged, tube deeply excavate ventrally. *Macroptera*: head with eyes and ocelli large, genae parallel; pronotum narrower than prothorax, epimeral setae capitate; fore wing parallel-sided but tapering to apex, without duplicated cilia; tergal wing-retaining setae weakly sigmoid (Fig. 50). *Micropterae* of both sexes intermediate in colour and structure between macropterae and apterae, with wing lobe 25–50 microns long.

Phallothrips houstoni Mound & Crespi

(Figs 48-50)

Phallothrips houstoni Mound & Crespi, 1992: 403.

Macropterous females are bicoloured, with the head dark brown, the pronotum yellow, the thorax and abdominal segments I–VIII light brown but segments IX–X yellow. The pronotum is narrower than the prothorax (Figs 48, 49), and only the epimeral setae are long and capitate. In contrast, apterae and micropterae of both sexes vary greatly in size. The smallest individuals are rather similar to macropterae in colour, but the more common larger individuals are robustly built with a massive thorax and fore legs, antennal segments almost moniliform, extensive reticulation on the thorax, and each tergite dark brown across the anterior half. The largest individuals have the epimeral setae small and pointed. In all forms, the mesopresternum and the pelta are effectively absent, and tergites II–VII each bear a single pair of long wing-retaining setae that are sigmoid only in macropterae (Fig. 50). This species is widespread across the semiarid areas of Australia, from Dalby and Goondiwindi in southern Queensland, across New South Wales to Broken Hill, and also South Australia at Leigh Creek and west of Whyalla. At these sites it has been found in the woody galls of *Iotatubothrips crozieri* on *C. cristata*. In Western Australia, colonies have been found in the woody galls induced by *Iotatubothrips kranzae* on *C. obesa* trees at the Murchison River crossing, 90km north of Geraldton.

Thaumatothrips Karny

Thaumatothrips Karny, 1922: 267. Type species Thaumatothrips froggatti Karny, by monotypy.

This genus is a member of the *Liothrips*-lineage of Phlaeothripinae (Mound & Marullo 1996), and the only known species shares most character states with the many species in the worldwide genus *Liothrips*. The species of

Liothrips are leaf-feeders and often induce leaf galls, although some, such as *L. piperinus*, invade the galls of various other Phlaeothripinae (Mound 2020), but whether as predators or as phytophagous kleptoparasites is not known. Karny described *T. froggatti* as a gall thrips, because it is found breeding in very large numbers in woody galls on certain *Casuarina* trees. However, subsequent studies (Mound & Crespi 1992) showed that two rather small and insignificant-looking species of *Iotatubothrips* induce the woody galls (Mound *et al.* 1998). *T. froggatti* is actually a phytophagous kleptoparasite within these woody galls. It is probably related to genera such as *Turmathrips* and *Warithrips*, that comprise gall-invading species on *Acacia* shrubs and trees (Crespi *et al.* 2004).

Diagnosis. Robust, macropterous and micropterous Phlaeothripinae with fore femora bearing row of teeth. Head longer than wide in macropterae, scarcely longer than wide in small males; postocular setae long and capitate, but vertex of micropterae with 2 pairs of very long slender setae; mouth cone short, rounded; maxillary stylets retracted to near postocular setae and close together medially. Antennae 8-segmented, relatively short, segment III with one sense cone, IV with 3 sense cones. Pronotum much narrower than prothorax; with 5 pairs of capitate major setae in macropterae, but 6 pairs of very long and slender setae in micropterae; notopleural sutures complete. Prosternal basantra absent; ferna large; mesopresternum reduced to 2 triangles; metathoracic sternopleural sutures long. Fore wings broad, with 12–18 duplicated cilia. Fore tarsal tooth massive (Fig. 47); fore femora swollen with 4 or 5 teeth on inner margin, fore tibial inner margin rugose. Pelta elongate-triangular but eroded and small in micropterae; tergites II–VII each with 2 pairs of sigmoid wing-retaining setae that are straight and long in micropterae; tergal lateral setae capitate in macropterae but very long and slender in micropterae; tergite IX setae about as long as tube; tube shorter than head. Male tergite IX S2 shorter than S1; sternites without pore plates.

Thaumatothrips froggatti Karny (Fig. 47)

Thaumatothrips froggatti Karny, 1922: 268

The macropterous and micropterous females of this species are strikingly different in appearance. The major setae on the head and pronotum are long and whip-like in micropterae, whereas they are shorter and capitate in macropterae. Moreover, female macropterae vary greatly in size, with small females having the head much less elongate. These variations were illustrated by Mound and Crespi (1992). This thrips has been found in the galls induced by the two different species of *Iotatubothrips* from eastern and western Australia. In eastern Australia, large colonies have been found in the woody galls of *Iotatubothrips crozieri* on *Casuarina cristata* at sites between Dalby and Goondiwindi in southern Queensland, also across inland New South Wales to Broken Hill. Specimens have also been seen labelled as collected by Froggatt in 1928 at Euston on the River Murray. In Western Australia, large colonies were found in the woody galls induced by *Iotatubothrips kranzae* on *Casuarina obesa* trees at the Murchison River crossing, 90km north of Geraldton.

Xyelethrips Mound

Xyelethrips Mound, 1970: 460. Type species Pygmaeothrips quadritibia Girault, by monotypy.

The original diagnosis of this genus was based solely on the female holotype of the only known species. Because of the elongate and convoluted stylets, this species was assumed to be associated with *Casuarina* trees. However, this assumption is probably incorrect, and the species is possibly fungus-feeding on the trunk of trees. The genus is not related to the other genera that are known to live on *Casuarina* species but shares most structural character states with members of the Plectrothripini (Okajima 1981). Antennal segment VIII is long and slender and constricted to a basal neck, and the sensorium on antennal segment II is in the basal half of that segment; there is one sense cone on segment III and two on IV both of which are placed ventrolaterally.

Diagnosis. Macropterous or micropterous Phlaeothripinae with long pointed mouth cone. Head wider at base than across eyes, genae with no prominent setae; eyes with less than 25 facets, postocular setae long and capitate; maxillary stylets very long, retracted to eyes, crossing over medially and with one convolution at base of head; mouth cone extending to mesosternum. Antennae 8-segmented, III with one sense cone, IV with 2 sense cones; II with

sensorium on basal half of segment, VIII slender and constricted to base. Pronotum with 5 pairs of major, capitate setae; notopleural sutures complete. Prosternal basantra and mesopresternum not developed; anterior margin of mesosternum eroded; metathoracic sternopleural sutures present. Fore tarsal tooth large. Fore wing parallel-sided, without duplicated cilia, with only one major sub-basal seta; micoptera wing-lobe about 70 microns long. Pelta broadly triangular; tergite II eroded laterally; II–VII each with a single pair of very long, curved wing-retaining setae, microptera without such setae; tergal lateral setae long; tube conical, anal setae short.

Xyelethrips quadritibia (Girault)

(Figs 74-78)

Pygmaeothrips quadritibia Girault, 1927a: 3

Six females of this species have been studied, taken at four different sites in northeastern Queensland in the region west of Rockhampton. Four of these females were taken by insecticide barkspraying of *Acacia harpophylla*, and as all four are micropterae this suggests that they were living on the trunk of the trees. The generic diagnosis given by Mound (1970) has been checked against each of the six specimens and remains valid, apart from an error in referring to the mesotergal lateral setae as "mesosternal". The micropterae differ from macropterae as follows: ocelli absent; metanotum transverse; fore wing lobe small, about 0.2 of thorax width; tergites without wing-retaining setae; tergite IX setae S1 capitate, shorter than tube and about as far apart as basal width of tube

Specimens studied. Holotype female macroptera, **Queensland**: Rockhampton, in forest, 13.iv.1923 (in QM). **Queensland**: Rockhampton 500km north, Redcliffe Tablelands, 2 female micropterae from barkspray of *Acacia harpophylla*, 18.iv.2012 (in QDPC); Rockhampton 400km southwest. Lake Nuga Nuga, 2 female micropterae from barkspray of *Acacia harpophylla*, 8.vi.2014 (in QDPC); Rockhampton 200km west, Blackwater, 1 female macroptera from *Eremophila*, iv.2007 (in ANIC).

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