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Host-shifts at family level in the Australian *Acacia*-thrips lineage (Thysanoptera, Phlaeothripinae) with two new species

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Abstract

The Australian *Acacia*-thrips lineage comprises at least 250 species in 30 genera of Phlaeothripinae, all of them known only from *Acacia* species in Australia. Two new species from two of these genera are described here as the first recorded instances of host-shifting within this diverse thrips lineage, with the host shifts being between unrelated angiosperm orders, from Fabales to Proteales and Myrtales. *Brakothrips eucalypti* **sp. n.** is described from the branches of a species of *Eucalyptus*, and *Katothrips banksiae* **sp. n.** is described forming substantial colonies within lepidopterous leaf mines on a species of *Banksia*. Previously these thrips genera were known only from *Acacia* species, and comprised seven described species of *Brakothrips* and 35 described species of *Katothrips*.

Key words: host-specificity, Fabaceae, Proteaceae, Myrtaceae, *Brakothrips*, *Katothrips*

INTRODUCTION

In Australia, one lineage of foliage-feeding thrips in the sub-family Phlaeothripinae has diversified into at least 250 species in 30 genera in association only with the plant genus *Acacia* (Crespi *et al*. 2004). Judging from specimens taken from *Acacia* plants, and slide-mounted at the Australian National Insect Collection, there are many more species in this lineage that are as yet undescribed. One genus in this lineage, *Kladothrips*, comprises species that induce galls on *Acacia* phyllodes, and some members of this genus have been the focus of study because they exhibit eusocial behaviour (Crespi 1992; Crespi & Yanaga 1995). One group of genera within this *Acacia*-thrips lineage comprises species that glue or sew together pairs of *Acacia* phyllodes and thus construct domiciles within which to breed (Gilbert & Simpson 2103; Gilbert *et al*. 2018). Furthermore, the thrips galls and domiciles on *Acacia* are both attacked by a diverse cohort of exploitative kleptoparasitic, but phytophagous, thrips species representing another nine genera within the *Acacia*-thrips lineage. However, most of the structural diversity within the *Acacia*-thrips lineage is found amongst 14 genera of what Crespi *et al*. (2004) refer to as "opportunist species". These are thrips that invade and breed in old galls and abandoned leaf-mines that were induced by various insects including Diptera, Hymenoptera and Lepidoptera. Genera such as *Akainothrips*, *Dactylothrips* and *Katothrips* each involve at least 50 species, many of which remain undescribed because they are known from only one or a few specimens.

A further suite of species within the *Acacia*-thrips lineage comprises small, usually wingless, dark brown and strongly sculptured species. These are found on live stems of various *Acacia* trees and shrubs with thin exfoliating bark, although they also occur sometimes in old galls. Referred to by Crespi *et al*. (2004) as the *Rhopalothripoides* group, 22 species have been described in six genera, including *Brakothrips*, *Corroboreethrips* and *Rhopalothripoides*, although several more species remain undescribed that are known from only a few specimens. The reason that so many species remain undescribed in this *Acacia*-thrips lineage is because descriptions need to be based on suitable samples that reflect the extensive intraspecific structural variation that is so common among such thrips species, also the need for reliable host-association data. Species in this *Acacia*-thrips lineage commonly have a restricted host range among the 1000 species of *Acacia* in Australia, and thus each tends to be localised and difficult to sample adequately.

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The purpose of the present account is to describe and discuss the significance of three thrips species that are clearly members of the *Acacia*-thrips lineage, but which are known to breed only on plants that are from two different angiosperm orders (Proteales and Myrtales) that are distantly related to the Fabaceae in the Fabales.

SPECIES ON NON-*ACACIA* HOST PLANTS

The first new thrips species described below is a member of the genus *Brakothrips*. Both sexes of this minute wingless species have been found under the exfoliating bark of young stems of *Eucalyptus cinerea* (Myrtaceae), a habitat essentially similar to that of the other species of *Brakothrips* but on a plant from a distantly related angiosperm order. The second new species is described below in the genus *Katothrips*. One member of this genus was described (Crespi *et al*. 2004) as *Katothrips hoarei* and based on two females that were taken from a leaf mine on *Banksia serrata* (Proteaceae). The significance of that association was not considered at the time of description, the specimens being assumed to be vagrants from some *Acacia* tree. However, more recent field work has confirmed the host association, with colonies of this thrips being found within Lepidoptera leaf-mines on the leaves of *Banksia integrifolia* at Melbourne Botanic Gardens. Also breeding in leaf mines on this tree species at the same site was a further and very different species of *Katothrips*. This was found subsequently at three widely separated sites and is described below as a new species.

The abandoned galls and leaf mines in which so many of the 'opportunist species' live, commonly show evidence of fungal attack, with the plant tissues in a moribund condition. It seems possible that host shifts might be facilitated by the thrips feeding, at least to some extent, on the products of fungal decay rather than the living cells of the host plant.

The tissues into which the thrips insert their feeding stylets are not known but, given the tissue invasion by micro-fungi the thrips are possibly mycophagous in part. Such a habit might be associated not just with host shifts, but with the remarkable radiation among the thrips with this opportunist behaviour. Purely phytophagous thrips such as the *Acacia* gall-inducers of the genus *Kladothrips* are commonly host-specific and have radiated into few species. In contrast, the genera of opportunists have evolved into a greater diversity of species, and these are associated with a wide range of *Acacia* species.

The lack of structural diversity within the small-bodied opportunist species on *Acacia* is a further interesting difference from the gall-inducing species. This lack of intra-specific structural diversity is presumably an indication of the absence of male/male competitive behaviour. However, some of the opportunist thrips species have developed chemical and physical defensive measures, presumably against the marauding ants that are ubiquitous on plants in Australia. For example, *Katothrips flindersi* is known to produce a chemical repellent from its anus when under attack, and *Dactylothrips* species have the last abdominal segment variously modified such that in *D. aenictus* it functions as a pair of pincers against two large tubercles on the preceding segment (Crespi *et al*. 2004).

Despite careful searching, none of the three thrips species discussed here has been found on any *Acacia* species, and the situation is interpreted as involving a host-shift from species of Fabaceae to species of Proteaceae and Myrtaceae. The purpose here is to describe the thrips species that are involved in these remarkable host-shifts.

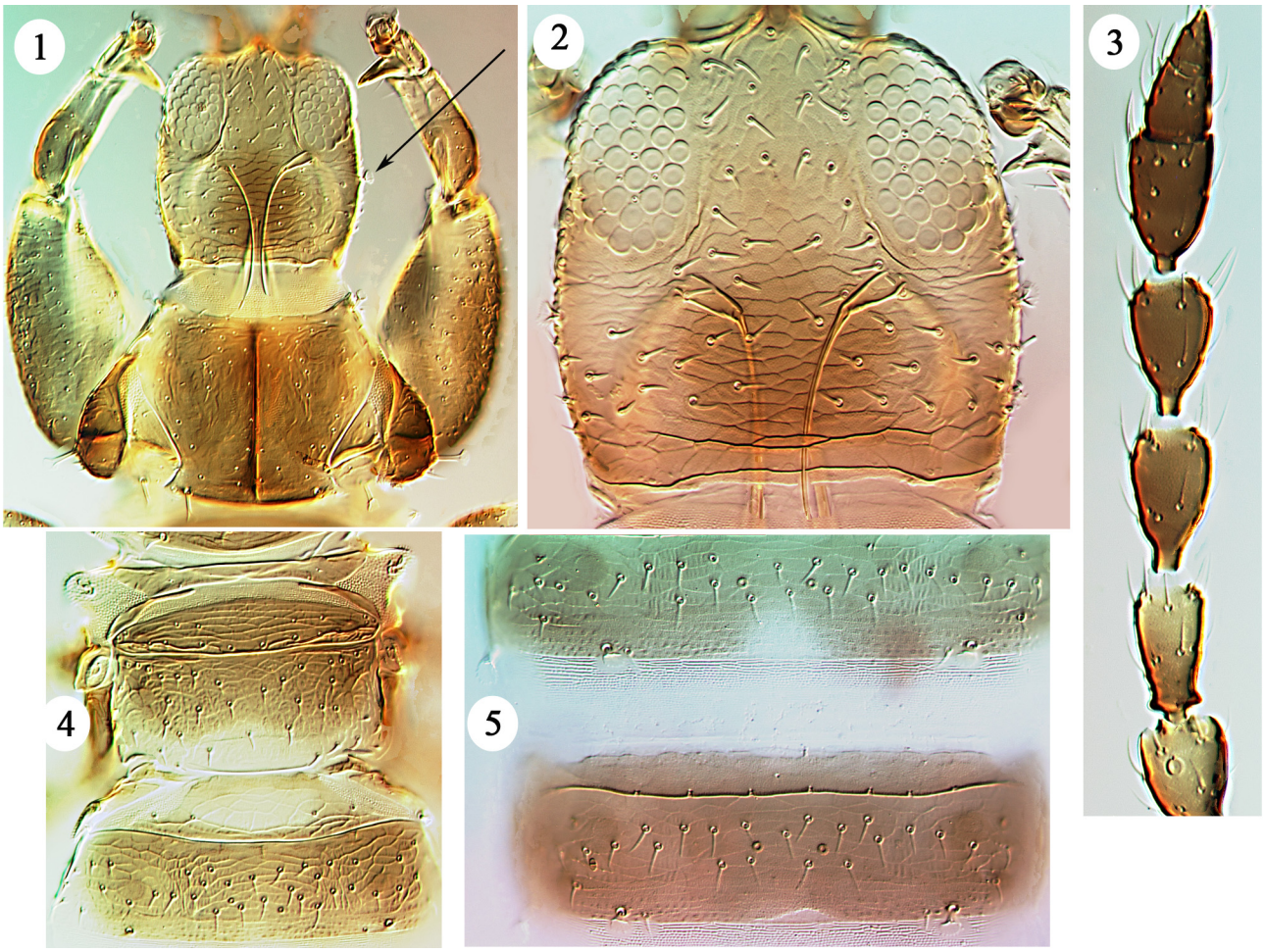
Material and methods

The photographic images were prepared using a Leica DM2500 DIC microscope and processed through Automontage and Photoshop. The specimens are slide-mounted in Canada balsam, and holotypes and other specimens are deposited in the Australia National Insect Collection (ANIC). The major setae on the pronotum are referred to as follows: am – anteromarginals; aa – anteroangulars; ml – midlaterals; epim – epimerals; pa – posteroangulars. The marginal setae on tergite IX are designated pairs S1, S2, S3, where S1 is the pair closest to the mid-line.

Brakothrips Crespi, Morris & Mound

This genus comprises seven described species (Crespi *et al*. 2004) with several further undescribed species known

only from isolated individuals. *Brakothrips* species have been found widely across the arid zone of Australia, between Port Augusta (South Australia), Barrow Island (Western Australia) and Blackall (Queensland), and a single male has been taken in eastern Tasmania. The seven species are small, dark brown, and wingless, with a characteristic basal flange to the third antennal segment, and each of them has the mouth cone long and pointed, extending beyond the fore coxae. These thrips are usually found by beating the fork between two small branches of an *Acacia* where the tissue is alive and the thin bark has split and left a small cavity. The adult thrips are minute, and larvae are not known for any species.



FIGURES 1–5. *Brakothrips eucalypti* **sp. n. (1)** head, pronotum and fore legs (arrow to po seta); **(2)** head; **(3)** antenna; **(4)** meso and metanotum, pelta and tergite II; **(5)** tergites V–VI.

Brakothrips eucalypti **sp. n.**

(Figs 1–5)

Male aptera. Body light brown with variable areas of yellow; head yellow laterally and between eyes, pronotum yellow laterally, also notopleura; pelta and posterior margin of metanotum yellow, also tergites II–III lateral margins; antennae brown with apical third of segment III yellow; tibiae with distal third or fifth yellow, femora variable. Head with compound eyes much larger dorsally than ventrally, ocelli absent (Fig. 2); vertex reticulate medially, with about 30 pairs of small setae including 2 longitudinal rows between the eyes; postocular setae arising on genae (Fig. 1), with apex as broadly expanded as setal length; mouth cone not extending beyond fore coxal hind margin. Antennae 8-segmented (Fig. 3), III with one sense cone, IV & V each with 2 sense cones; VII & VIII closely joined, VII broadly joined to VI, IV–VI sharply pedicillate, III with basal flange over pedicel. Pronotum with many short stout setae, with 3 or 4 pairs of short, capitate major setae, midlateral pair variable, anteromarginal pair not developed; notopleural sutures complete. Fore femora and fore tarsal tooth of largest male enlarged (Fig. 1), but these are more slender in small males. Mesonotum slender, transverse, lateral setae minute. Metanotum irregularly reticulate with

at least 40 small bluntly pointed setae (Fig. 4). Prosternal basantra absent, ferna transverse and fused medially; mesopresternum absent or reduced to pair of small lateral triangles, mesoeusternal anterior margin entire. Pelta transverse, reticulate on posterior third (Fig. 4); tergite II with about 40 bluntly pointed discal setae, III–VIII with fewer discal setae and these are more acute on the more posterior tergites; II–VII each with pair of short, broadly capitate posteromarginal setae and mesad of these a pair of small curved marginal setae (Fig. 5); tergite IX setae S1 and S2 capitate, shorter than basal width of tube, S3 long and acute.

Measurements (holotype male in microns). Body length 1350. Head, length 175; maximum width 160; postocular setae 10. Pronotum, length 150; width 190; major setae, aa 15; epim 25, pa 25. Tergite IX setae, S1 25; S2 25; S3 100. Tube length 125. Antennal segments III–VIII length, 45, 48, 45, 45, 25, 23.

Female aptera. Similar to male in colour and structure; length of fore tarsal tooth less than half tarsal width.

Material examined. *Holotype* male aptera, **AUSTRALIA, Australian Capital Territory**, Weston, Oakey Hill (35°20′16″S, 149°04′05″E), from young exfoliating twigs of *Eucalyptus cinerea*, 21.iv.2011 (LAM5494).
Paratypes: taken with holotype, 5 females, 2 males; from same tree as holotype, 5 females, 3 males, 18.ii.2012 (LAM5553).

Comments

In the key to the seven described species of this genus (Crespi *et al*. 2004) this new species tracks to *stenos*, because antennal segments VI–VIII form a single unit, with VII broadly attached to VI and not constricted into a basal neck. However, all the previously described species in this genus, including *stenos*, are entirely dark brown, whereas this new species has antennal segment III yellow distally, and the body is light brown with yellow areas laterally as well as yellow areas on the legs. In contrast to the other species, the mouth cone does not extend beyond the fore coxae, and the pronotum has the anteromarginal pair of setae no longer than the discal setae. Antennal segment III in *stenos* bears no sense cones, but this segment in *eucalypti* bears a single well-developed sense cone. A unique feature of this species is the presence of a pair of short broadly capitate setae on the lateral margins of the head (see arrow on Fig. 1). These setae are possibly homologous with the postocular setal pair that occurs in typical Phlaeothripidae, but their position far behind the eyes and laterally on the genae appears to be unique. In addition to the type series from Canberra, two very similar females have been seen from *Eucalyptus wandoo* south of Perth in Western Australia, but these have the tenth abdominal segment more uniformly brown than the types.

Katothrips Mound

This genus was erected for six species from *Acacia* trees in Australia (Mound 1971), but Crespi *et al*. (2004) subsequently included 35 species in the genus. However, judging from the available slide collections there are at least a further 15 undescribed species. These thrips all live in cryptic situations on various *Acacia* species, such as in abandoned leaf-mines and galls. They exhibit a high degree of host-plant specificity, and the species considered to be members of this genus exhibit considerable structural diversity. In the absence of any molecular data there is no clear evidence that these species represent a single lineage, but generally they have the antennal sense cones in an unusual ventral rather than lateral position. Some of them are similar in structure to species of *Dactylothrips* with strongly reinforced posterior segments to the abdomen. However, they lack the elongate mandible found in *Dactylothrips* species, and the similarities presumably represent convergence due to occupying similar niches on *Acacia* trees and having similar behaviour for avoiding ant predation.

Katothrips hoarei Crespi, Morris and Mound
(Figs 13–15)

Katothrips hoarei Crespi, Morris and Mound, 2004: 212.

Based on two females taken in southeastern Australia from a lepidopterous leaf-mine on *Banksia serrata*, four fur-

ther females have been collected more recently from leaf-mines on *Banksia integrifolia*. The species is unusual in having all five pairs of pronotal major setae fully developed, a condition amongst *Katothrips* species that is known only in *K. echinatus* and the new species described below. Moreover, *hoarei* is unique in the genus in having two sense cones on the third antennal segment (Fig. 13), not just a single one. The body colour of mature specimens is remarkable, being essentially yellow with pairs of dark brown spots laterally on tergites III–VIII (Fig. 15), also laterally on the meso and metathorax and sub-medially on the pronotum (Fig. 14); the mid tibiae are brown at the base, and the hind femora brown at the apex.

Material examined. Holotype and paratype female macropterae, **AUSTRALIA, Victoria**, Croajingolong NP, from lepidopterous leaf mine on *Banksia serrata*, 31.viii.1995 (R. Hoare). **Victoria**, Melbourne Botanic Gardens, 4 females from leaf mines on *Banksia integrifolia*, iv.2012 (L. Semeraro).

Katothrips banksiae sp. n.

(Figs 6–12)

Female aptera. Body and legs pale yellow, tube darker yellow; antennal segments I–II yellow, III sometimes weakly shaded, IV–VIII increasingly brown; major setae all translucent. Head longer than wide, weakly constricted behind eyes (Fig. 6); head without ocelli, with weak reticulation on lateral thirds, eyes slightly smaller ventrally than dorsally; 2 pairs of postocular setae, one pair placed laterally; maxillary stylets rather broad, retracted at least to postocular setae, close together medially but diverging posteriorly in the unusually broad mouth cone; maxillary guides stout; maxillary palps short, labial palps with prominent stout sense cone apically. Antennae 8-segmented (Fig. 12), III–V each with one short stout sense cone ventro-laterally. Pronotum without sculpture (Fig. 7), with 5 pairs of capitate major setae; notopleural sutures sometimes incomplete. Fore legs stout with tarsal tooth pointed and about as long as tarsal width. Prosternal basantra and mesopresternum absent, ferna weakly sclerotised, mesoeusternal anterior margin deeply eroded (Fig. 10). Mesonotum transverse, lateral setae capitate. Metanotum without sculpture or major setae (Fig. 8). Pelta transverse, weakly sculptured (Fig. 9); tergites II–VII with one pair of capitate setae posterolaterally, VIII–IX each with 2 pairs; tube shorter than head width, anal setae longer than tube. Sternites with 4–6 small discal setae, posteromarginal setae S1 unusually long, much longer than length of their sternite.

Measurements (holotype female in microns). Body length 1800. Head, length 185; maximum width 150; postocular setae 25. Pronotum, length 150; width 230; major setae, am 25, aa 30; ml 30, epim 33, pa 33. Tergite IX setae, S1 60; S2 55; S3 180. Tube length 100. Sternite VII posteromarginal setae S1 length 150. Antennal segments III–VIII length, 40, 38, 38, 38, 40, 23.

Female macroptera. Similar in colour and structure to aptera; head with ocelli present; metanotum with 2 to 6 small setae medially; tergites II–VII each with one pair of long, weakly sigmoid wing-retaining setae; fore wings parallel sided, without duplicated cilia, with two short capitate basal setae.

Male aptera. Similar in colour and structure to female aptera, slightly smaller; tergite IX setae S2 pointed and stout; sternite VIII with no pore plate.

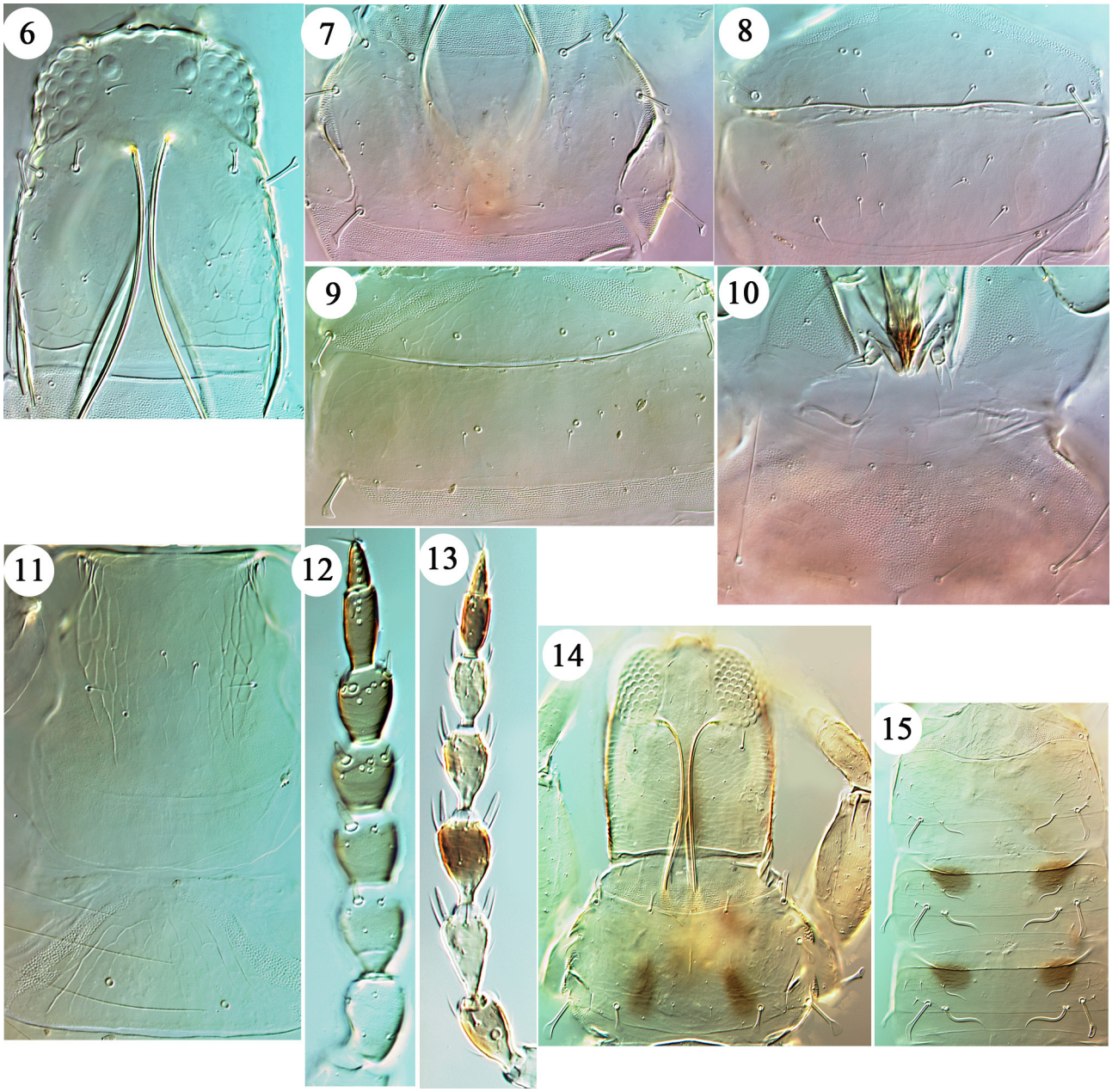
Material examined. Holotype female aptera, **AUSTRALIA, New South Wales**, Pebbly Beach, 20km north of Bateman's Bay (35°31'43"S, 150°10'50"E), from leaf mine on *Banksia integrifolia*, 12.xi.2012 (LAM5620).

Paratypes (apterae except where stated): 8 females, 2 males (with larvae and pupae) taken with holotype; same locality but 13.xi.2019, 1 female macroptera, 10 females, 1 male; Moruya Heads, 30km south of Bateman's Bay, 12.xi.2012, 1 female from leaf mines on *Banksia integrifolia*; same locality and host, 2.i.2013; 1 macropterous female, 2 females, 3 males. **Victoria**, Melbourne, Royal Botanic Gardens, iii-iv.2012, 3 female macropterae, 4 females, 4 males (with larvae) from leaf mines on *Banksia integrifolia*, (L. Semeraro).

Comments

This species has antennae that are unlike those of any other member of the genus, and seem to be poorly developed, almost larviform (Fig. 12). The pronotum bears five pairs of major setae, a condition found in only two other *Katothrips* species, as noted above. The prosternal sclerites are particularly weakly sclerotised (Fig. 10), although there are other species in the genus with a rather similar condition, such as *K. enochrus*. Similarly, the maxillary stylets

are unusually long and stout (Fig. 6), but similar stylets occur in a few other members of the genus, including *K. tagacis*. No other member of the genus has two pairs of capitate postocular setae, with the second pair lateral to the usual pair, and the only congeners with a single sense cone on the fourth antennal segment are *K. uniconus* and the micropterae of *K. biconus*. In contrast to many members of the genus, the males of this new species lack a sternal pore plate, and the sternites of females have none of the iridescent reticulation that is found in several species. Most species of *Katothrips* have been collected as individuals or in small samples (Crespi *et al*. 2004). In contrast, considerable populations of this new species, including all life stages, have been found in both young and old leaf mines caused by Lepidoptera (?Nepticulidae). However, as is common among members of this genus there is limited sexual dimorphism, and no indication of the social behaviour found amongst some of the gall-inducing thrips on *Acacia* species.



FIGS 6–15. *Katothrips* species. *K. banksiae* **sp. n.** 6–12: **(6)** head; **(7)** pronotum; **(8)** meso and metanotum; **(9)** pelta and tergite II; **(10)** prosternites; **(11)** macroptera metanotum and pelta; **(12)** antenna. *K. hoarei* 13–15: **(13)** antenna; **(14)** head and pronotum; **(15)** pelta & tergites II–IV.

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