



## Predation, phytophagy and character state confusion among North American species of the genus *Leptothrips* (Thysanoptera: Phlaeothripinae)

LAURENCE MOUND<sup>1</sup> & CHERYLE O'DONNELL<sup>2</sup>

<sup>1</sup>Australian National Insect Collection, CSIRO, Canberra, Australia. E-mail: [laurence.mound@csiro.au](mailto:laurence.mound@csiro.au);

<sup>2</sup>USDA-APHIS-PPQ-National Identification Services; Beltsville, MD. USA. E-mail: [cheryle.a.odonnell@aphis.usda.gov](mailto:cheryle.a.odonnell@aphis.usda.gov)

### Abstract

Difficulties are discussed of specimen preparation, of character state variation, and of species recognition in the genus *Leptothrips*, also the extent to which some of the species are phytophagous rather than predatory. An identification key is provided to 15 *Leptothrips* species from North America. Nine species described by Johansen (1987) are newly placed into synonymy, a further unrecognisable species is based on a single deformed specimen, and *L. texcosensis* Johansen-Naime *et al.* (2017) is transferred to the genus *Haplothrips*.

**Key words:** synonymies, predation, phytophagy, character state variation

### Introduction

Predation by the thrips species that are now treated in the genus *Leptothrips* was first recorded by Fernald (1892), who reported that larvae of *Phloeothrips mali* were observed feeding on the eggs of the Gypsy Moth. Fitch (1855) had described *mali* from New York as the Apple Thrips, commenting that it had been found in small pea-sized cavities on apples that had failed to mature properly, and suggesting that the thrips might be the cause of these cavities. However, observations gradually accumulated on the predatory habits of this black thrips with distinctive purple internal pigments, and Bailey (1940) summarised many of these reports. Bailey reported seeing adults and larvae of *mali* feeding on the eggs and crawlers of the scale insect, *Lecanium corni*, and referred to it as feeding on the eggs of certain moths, as well as mites (particularly eriophyids), red spider eggs, and the larvae of other thrips species (including eliminating caged populations of *Frankliniella occidentalis* and *Drepanothrips reuteri*). As a result, predation by *Leptothrips* species has become assumed to be general, although as with other broad generalisations about thrips biology, this assumption needs further substantiation.

The only extensive study on the biology of any member of the genus was on the Black Hunter, *Leptothrips mali*. For this species, Parrella *et al.* (1982) demonstrated that development from first instar to adult was 18 days when the mite, *Panonychus ulmi*, was available as prey, but 23 days when the thrips was raised on apple pollen. Wiesenborn (2015), in a careful study on the phenology of *L. larreae*, stated that the most likely food for larvae and adults was mites that inhabited the cecidomyid galls in which this thrips breeds on the plant, *Larrea tridentata*. In contrast, Wiesenborn (2012) studied *L. fasciculatus* on its host plant, *Eriogonum fasciculatum*, and recognised that the population he studied was anthophilous. However, given the evidence from Parrella that *mali* can survive on pollen without access to prey, it is possible that other species of *Leptothrips*, including *L. fasciculatus*, are more opportunistic in their behaviour than has been considered, and that this depends on the food source available. Certainly, some species of *Leptothrips* are occasionally collected in larger numbers than might be expected for a predator. There is a possibility that *Leptothrips* species may be similarly flexible in their feeding behaviour to thrips such as *Frankliniella occidentalis*, *Frankliniella schultzei*, and *Thrips tabaci*, all of which are phytophagous but are known to be effective predators under some circumstances. Predation seems to be a behaviour that has been adopted opportunistically by a few species within several unrelated Thysanoptera genera, and in very few genera are all species obligate predators, such as *Scolothrips* [Thripidae] and *Frankliniothrips* [Aeolothripidae].

## Problems in species recognition

Any potential of *Leptothrips* species as biological control agents is limited by several factors that render difficult the identification of individual species within the genus. First, there is considerable structural uniformity among individuals across species, despite curious variation in a few characters between individuals of single populations. Second, the described species were based mainly on few specimens, with no information on intra-specific variation, and with no support from observations on biology. Finally, the taxonomic literature on the genus is mainly 80–100 years old, and conclusions in the only modern study (Johansen 1987) are here considered unreliable.

Johansen (1987) provided keys to 41 species, of which 22 were described as new. The 41 species were segregated into the following five “Groups”. Two groups were distinguished because the fore tarsus of females bears a small tooth, whereas females of the remaining species of *Leptothrips* lack such a structure. Group Primarius comprised two species from Mexico, but both of these were transferred subsequently by Mound and Marullo (1996) to the genus *Haplothrips*. Group Distalis comprised five species of which three from North America are considered below. Of the remaining 34 species, four Neotropical species, that are not considered further here, have a dark longitudinal marking on the fore wing and were segregated as Group Astutus. The final two, Group Mali and Group Obesus, thus comprised 30 species with hyaline fore wings, and these two groups were distinguished from each other as follows:

“Group Mali” with 25 species—cuerpo esbelto; cabeza esbelta, discreta a notablemente más larga que ancha; tubo notablemente ensanchado en su base, luego angostado y paulatinamente más angosto en sentido posterior; [body and head slender, head scarcely to distinctly longer than wide; abdominal tube significantly widened at base then gradually narrowed posteriorly].

“Group Obesus” with 5 species—cuerpo robusto; cabeza robusta, discretamente más larga que ancha o casi tan larga como ancha; tubo conico corto, de base ancha y lados rectos [body and head robust, head scarcely longer than wide or almost as long as wide; abdominal tube short conical, base wide and sides straight].

There are major problems with recognising these two groups. It is not just that the wording of the differences is too subjective to be functionally effective in identifying individual specimens. More importantly, among the five species of Group Obesus, *gurdus*, *opimus*, and *robustus* are all slide-mounted in clarite, and are heavily crushed with the shape of the head and tube distorted (Figs 7–9; 14–16). Similarly, the original illustration of *obesus* (Johansen, 1987; Fig. 61) seems likely to have been based on a specimen that was under undue cover-slip pressure. Moreover, the illustration of *cassiae* (Johansen, 1987; Fig. 49) is of a rather bulbous head that contrasts with the illustration here of a good slide-mount of this species (Fig. 1). The subjective nature of the proposed differences is clear from the tube of *gurdus* (Fig. 14) (in Group Obesus) that is scarcely different from that of *mali* (Fig. 10) (in Group Mali), whereas *brevicapitis* (= *oribates*) (Fig. 13) was placed in Group Mali despite having the tube more clearly short and conical. A further complication is that the tube is sometimes slightly longer in males than females (Figs 10, 11), and the published wording fails to take into account any sexual difference. We therefore conclude that Group Obesus and Group Mali are not valid segregates.

Within “Group Mali” Johansen recognised three “Series”, based on the species *oribates*, *mali* and *pini*, with 10, 12 and 3 species respectively. The “Series Pini” was diagnosed as having antennal segment IV with only two sense cones—one inner and one outer. In contrast, “Series Oribates” was diagnosed as having two inner and two outer sense cones on segment IV with “one small accessory [cone] optional”, whereas “Series Mali” was diagnosed as having antennal segment IV with one large sense cone at the inner apex and two at the outer apex with “one small accessory cone optional”. However, this assessment of the condition in the latter two Series is not valid. Not only do specimens (in BMNH) identified by Johansen as *mali* have two major sense cones on both inner and outer apices of antennal segment IV, but this condition is normal amongst North American specimens identified as *mali* by several other workers, including Bailey, Hood, Parrella and Stannard. The conclusion by Johansen is particularly confusing, in that specimens from the population of *mali* at Nelson, Virginia, of which the biology was studied by Parrella *et al.* (1982), were segregated by Johansen into three species. These were *mali*, plus two new species that he placed in “Series Oribates” as *maliaffinis* and *septemtrionalis*. As indicated by Hoddle *et al.* (2012), no evidence was produced that Parrella had worked on a mixed population of more than one species. The conclusion by Johansen was based solely on the claim that there was either one or two major sense cones on the inner apex of antennal segment IV. However, all of the available specimens from the Parrella study, including those

identified as *mali*, *maliaffinis* and *septemtrionalis*, have two major sense cones at the inner apex of antennal segment IV. It is not unusual for one of these sense cones to be about half the length of the other, but even so, they are both clearly *sensilla basiconica*, as discussed below under Character States, and clearly distinct from the minute *sensillum coeloconicum* that sometimes occurs on the external surface of this segment. These observations not only indicate that Series Oribates and Series Mali are not valid segregates, but they call into question the validity of several of the 22 new species of *Leptothrips* described by Johansen. The limited objective of the present study, however, is to re-assess the *Leptothrips* species listed from North America. In attempting to produce a functional identification key we emphasise below the exceptional technical problems involved in slide-mounting members of this genus.

## Collections and character states studied

This work is based on a re-examination of all the relevant type specimens, including those of species at The Natural History Museum, London (BMNH) that were described by Johansen, also the extensive slide collections at the United States National Museum of Natural History, Washington (USNM), together with almost 1000 slides from the Entomology Research Museum, University of California, Riverside (ERMUR). These long series enabled a re-assessment, within single population samples, of the variation in several character states that have been used previously in species delineation in this genus.

The technical problems we have experienced in studying *Leptothrips* species seem greater than with almost any other genus of Thysanoptera. Okajima and Masumoto (2014) emphasised that taxonomic decisions in the Phlaeothripinae genus *Azaleothrips* must be based on specimens that have been slide mounted each to an equally high standard, and this constraint also applies to *Leptothrips* species. Unfortunately, as a result of extensive purple internal pigments, the sculpture on the pronotum is scarcely visible unless the body contents have been removed. However, removal by chemical treatment can lead to loss of character states on the fore wings unless great care is taken. Many specimens of this genus in museum collections cannot be identified satisfactorily because the pronotal sculpture is not visible, or the wings are crumpled. Moreover, the membrane between antennal segments IV–V often collapses and thus hides one or more of the sense cones at the apex of IV. As indicated by Figures 7–9 and 14–16, gross changes to body form are produced through inexpert slide preparation.

The following are the main characters that have been assessed in this study:

*Antennal segment III sense cone:* The size of this sense cone varies between species and is much smaller than is usual in Phlaeothripidae. It is commonly scarcely 12 microns in length, and in no species more than 15 microns. Moreover, it is not stout in any species, and is often unusually slender. In two species, *larreae* and *purpuratus*, this sense cone cannot be seen and is interpreted as being absent.

*Antennal segment IV sense cones:* Johansen (1987) uses the following two terms: “cono sensorial grande” and “cono pequeno accesorio” [large sense cone and small accessory sense cone]. The first of these is here interpreted as referring to the typical sense cones of Phlaeothripidae, *sensilla basiconica*, that occur near the apex of antennal segment IV. The second is interpreted as the *sensillum coeloconicum* that sometimes occurs on the external margin of segment IV, arising almost between but slightly basal to the bases of the two major sense cones. This structure is about 6 microns in length, and its presence or absence is sometimes difficult to determine on one or both antennae. These technical terms for sense cones are those used by De Facci *et al.* (2011).

*Length and colour of antennal segments:* Striking differences in colour and length of segments III and IV are frequently observed between individuals, but because variation occurs within single samples these differences were not used in this study. This is also mentioned below under *mali* and *papago*.

*Maxillary stylets position:* There are clear differences in the position within the head of the maxillary stylets between certain species (see Figs 1–5). But generally it has not proved possible to correlate precise stylet positions with putative taxa due to the extent with which these stylets become dissociated in *Leptothrips* species during typical slide-mounting procedures.

*Ventral prolongation of compound eyes:* For this character state to be compared it is essential that the head is slide-mounted horizontally - that is with the fore ocellus clearly overhanging the inter-antennal projection. If the inter-antennal projection projects anterior to the first ocellus, then the head is not truly horizontal, and any ventral prolongation of the eyes is less obvious. Conversely, if the fore ocellus greatly overhangs the inter-antennal

projection then the anterior margin of the head is tilted downwards, and the ventral prolongation of the eyes considerably increased.

*Pronotal sculpture lines*: The dense purple internal pigment that is typical of *Leptohiprips* species renders it difficult or even impossible to see transverse striae on the pronotum unless the specimen is cleared. In some of the Western species, these striae are particularly closely spaced and strongly defined (Figs 19, 20). In contrast, there are some species that lack striae on at least the median area of the pronotum (Figs 21–23). Unfortunately, the situation in *mali* involves an intermediate condition, with the striae continuous but weaker and more widely spaced medially (Figs 17, 18).

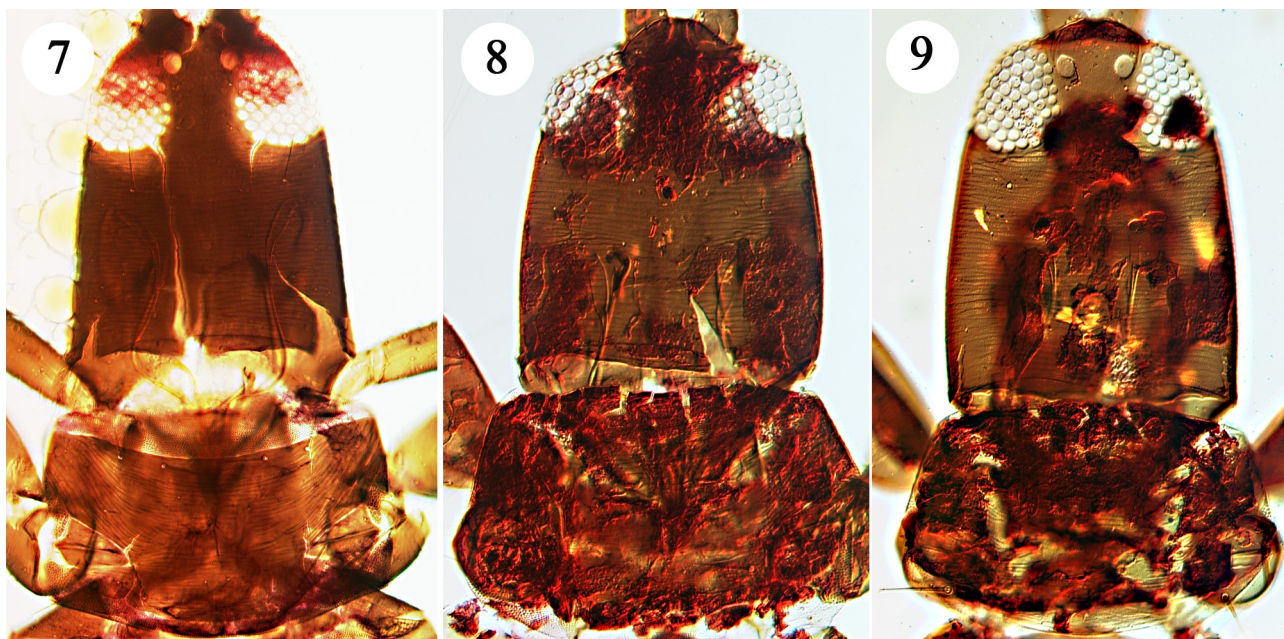


**FIGURES 1–6.** *Leptohiprips* species of North America. (1) *cassiae*; (2) *mali*; (3) *pini*; (4) *purpuratus*; (5) *occipitalis* holotype; (6) *opimus* holotype, antennal segments I–III.

*Fore wing duplicated cilia*: The presence or absence of these cilia appears to be unstable in some species, with the presence and number often differing on left and right wings of the same individual. The condition in *papago* and *fasciculatus* is apparently consistent, with the fore wing lacking any duplicated cilia. However, in the Western species *heliomanes* the duplicated cilia are particularly variable, commonly being absent on both wings, but sometimes present although unusually slender and dark, and occasionally well-developed on at least one wing. Similarly, in *larreae* the number of duplicated cilia commonly varies between left and right wings, although complete absence seems to be rare in this species.

*Tube length and shape*: There is considerable difference in the length and shape of the tube between some species, such as *mali* and *oribates* (Figs 10 & 13), and also between sexes (Figs 10, 11). However, the tube is easily distorted by cover-slip pressure, particularly with water soluble mountants such as clarite, as discussed above (Figs 14–16).

**Species-groups**. Based on the character states discussed above, four groups of species can be distinguished amongst the *Leptothrips* of North America. Two species, *pini* and *singularis*, have only two sense cones on the fourth antennal segment, whereas all the other species have three or four. Three species share the presence of a fore tarsal tooth, *distalis*, *fasciculatus* and *purpuratus*, but as noted below there are some surprising differences between these three species. A further three species lack a fore tarsal tooth and have no major sculpture lines on the pronotum, at least medially; these are *cassiae*, *macrocellatus* and *oribates*. Finally there is the group of species that lack a fore tarsal tooth but have the pronotum with strong transverse sculpture lines, and this involves the largest number of available specimens. It is amongst this group of five species that species concepts are particularly doubtful: *heliomanes*, *larreae*, *mali*, *papago* and *primigenus*. Despite the presence of individuals that are intermediate in structure between two or more of these segregates, the majority of available specimens fall into one or other of these five groups using the discriminants in the key below. However, one species, *occidentalis*, does not fall into any of these groups. It has elongate maxillary stylets, rather like *purpuratus*, but lacks a fore tarsal tooth. In contrast, it shares with *heliomanes* the absence of fore wing duplicated cilia and the presence of strong pronotal striae.



**FIGURES 7–9.** *Leptothrips* species of North America, head and pronotum. (7) *gurdus* holotype; (8) *opimus* holotype; (9) *robustus* holotype.

### ***Leptothrips* Hood**

*Leptothrips* Hood, 1909: 249. Type species *Cryptothrips aspersus* Hinds 1902, by monotypy; synonym of *Phloeothrips mali* Fitch.

Members of this genus share character states with other Phlaeothripinae species in the Tribe Haplothripini (Mound & Minaei 2007): antennae usually 8-segmented; head usually with maxillary bridge present; prosternum with paired basantra (praepectal plates); fore wings usually slightly constricted medially. From other Haplothripini the genus is distinguished by the presence of longitudinally striate sculpture on the metanotum (Figs 25–30). Prior to this study a total of 38 species were listed in this genus (ThripsWiki 2017), but nine of these species are here placed into synonymy. Moreover, a recently described species, based on a single male specimen, *L. texcosensis* Johansen-Naime *et al.* (2017), is here recognised as a species of *Haplothrips*. It shares with two other species that also were described as members of *Leptothrips* Group Primarius (see discussion above) the presence of equiangular reticulate sculpture on the metanotum. This species is thus referred to as *Haplothrips texcosensis* Johansen-Naime *et al.* **comb.n.**

### Key to the *Leptothrips* species from North America

1. Fore tarsus of female with small or minute tooth on inner margin . . . . . 2
- Fore tarsus of female without a tooth on inner margin . . . . . 4
2. Fore wing with 6–10 duplicated cilia; antennal segment III with one sense cone; pronotal mid-lateral setae present . . . *distalis*
- Fore wing without duplicated cilia; combination of other characters different . . . . . 3
3. Pronotum without any lines of sculpture medially; antennal segment III with one sense cone; antennal segments IV–VI uniformly brown; pronotal mid-lateral setae present (Fig. 22) . . . . . *fasciculatus*
- Pronotum medially with closely spaced transverse sculpture lines; antennal segment III with no sense cone; antennal segments IV–VI largely yellow; pronotal mid-lateral setae absent (Fig. 24) . . . . . *purpuratus*
4. Pronotum medially with prominent sculpture lines . . . . . 5
- Pronotum with a few striae laterally and near posterior margin, but sculpture lines medially either absent or very weak . . . . 11
5. Antennal segment II asymmetric with apical margin oblique (Fig. 6) . . . . . *opimus*
- Antennal segment II symmetric, apex transverse . . . . . 6
6. Antennal segment III with no sense cone, length of segment III usually no more than sub-equal to length of segment II; length of antennal segments III+IV no more than 125 microns [fore wing with number of duplicated cilia varying from 0–6]; apparently host specific to *Larrea tridentata* . . . . . *larreae*
- Antennal segment III with one sense cone; length of antennal segments III+IV usually more than 140 microns . . . . . 7
7. Antennal segment IV with four major sense cones . . . . . 8
- Antennal segment IV with three major sense cones . . . . . 10
8. Maxillary stylets retracted into head to level of postocular setae, and close together medially (Fig. 5) . . . . . *occidentalis*
- Maxillary stylets retracted about half way to postocular setae and wide apart (Figs 1–3) . . . . . 9
9. Fore wing with 5 or more duplicated cilia; pronotal striae weak and widely spaced medially . . . . . *mali*
- Fore wing usually without, or with very few duplicated cilia; pronotal striae strongly developed . . . . . *heliomanes*
10. Fore wing with duplicated cilia present . . . . . *mconelli*
- Fore wing not known to have any duplicated cilia . . . . . *papago*
11. Antennal segment IV with 2 sense cones . . . . . 12
- Antennal segment IV with 3 or 4 sense cones . . . . . 13
12. Pronotum as dark as head, hind tibiae uniformly dark brown . . . . . *pini*
- Pronotum paler than head, hind tibiae yellow distally . . . . . *singularis*
13. Antennal segment IV with three major sense cones . . . . . *macrocellatus*
- Antennal segment IV with four major sense cones . . . . . 14
14. Antennal segment IV without a small ancillary sense cone . . . . . *oribates*
- Antennal segment IV with a small ancillary sense cone on outer margin . . . . . *cassiae*

### *Leptothrips cassiae* (Watson)

*Haplothrips cassiae* Watson, 1920: 23

Known only from Florida, this is one of the species that lacks transverse striae medially on the pronotum. Johansen (1987) placed *cassiae* in his “Group Obesus” and thus distinguished it from *mali* on the basis of the claimed differences in the shape of the tube discussed and illustrated above. Almost no structural difference has been detected between specimens identified as *cassiae* from Southeastern USA, and specimens identified as *oribates* from Southwestern USA. These two species have the mesonotal transverse striae (Fig. 1) more widely spaced than in *mali*. However, a single female (in ERMR) from Venezuela has been studied that has the mesonotum closely striate but otherwise shares the character states of *cassiae*.

### ***Leptothrips distalis* (Hood)**

*Haplothrips distalis* Hood, 1925: 103.

*Zygothrips californicus* Mason, 1926: 156. Synonymy in Cott, 1956: 101.

*Leptothrips pristinus* Johansen, 1987: 33. **Syn. n.**

This is another member of the genus known only from the western States. It is one of the few species in the genus with a small tooth on the inner margin of the fore tarsus, but is distinguished from two other species with this structure by the presence of several duplicated cilia on the fore wing. The pronotum bears transverse striae, the pronotal mid-lateral setae are present as in *fasciculatus*, but the mesonotum is closely striate in contrast to that species (Fig. 28). Cott (1956: 103) indicated that *distalis* had been found breeding in large numbers on a species of *Atriplex* at Firebaugh (near Fresno) in California. He stated that the plants were severely damaged by this thrips, and made no reference to the possibility that it might be predatory. Johansen described *pristinus* from Baja California, and distinguished it because of the presence on antennal segment IV of a small accessory sense cone on the external margin. However, as discussed above, the presence of these minute *sensilla coeloconica* appears to be unstable in some species, and examination of a paratype of *pristinus* (in USNM) suggests that this species cannot be distinguished satisfactorily from *distalis*.

### ***Leptothrips fasciculatus* (Crawford DL)**

*Phyllothrips fasciculata* Crawford DL, 1909: 105.

*Phyllothrips fasciculata* var. *stenoceps* Crawford DL, 1909: 108.

*Anthothrips nigricornis* Jones, 1912: 17.

*Haplothrips jonesi* Karny, 1912: 344. Replacement name for *nigricornis* Jones, a homonym of *nigricornis* Bagnall, 1910.

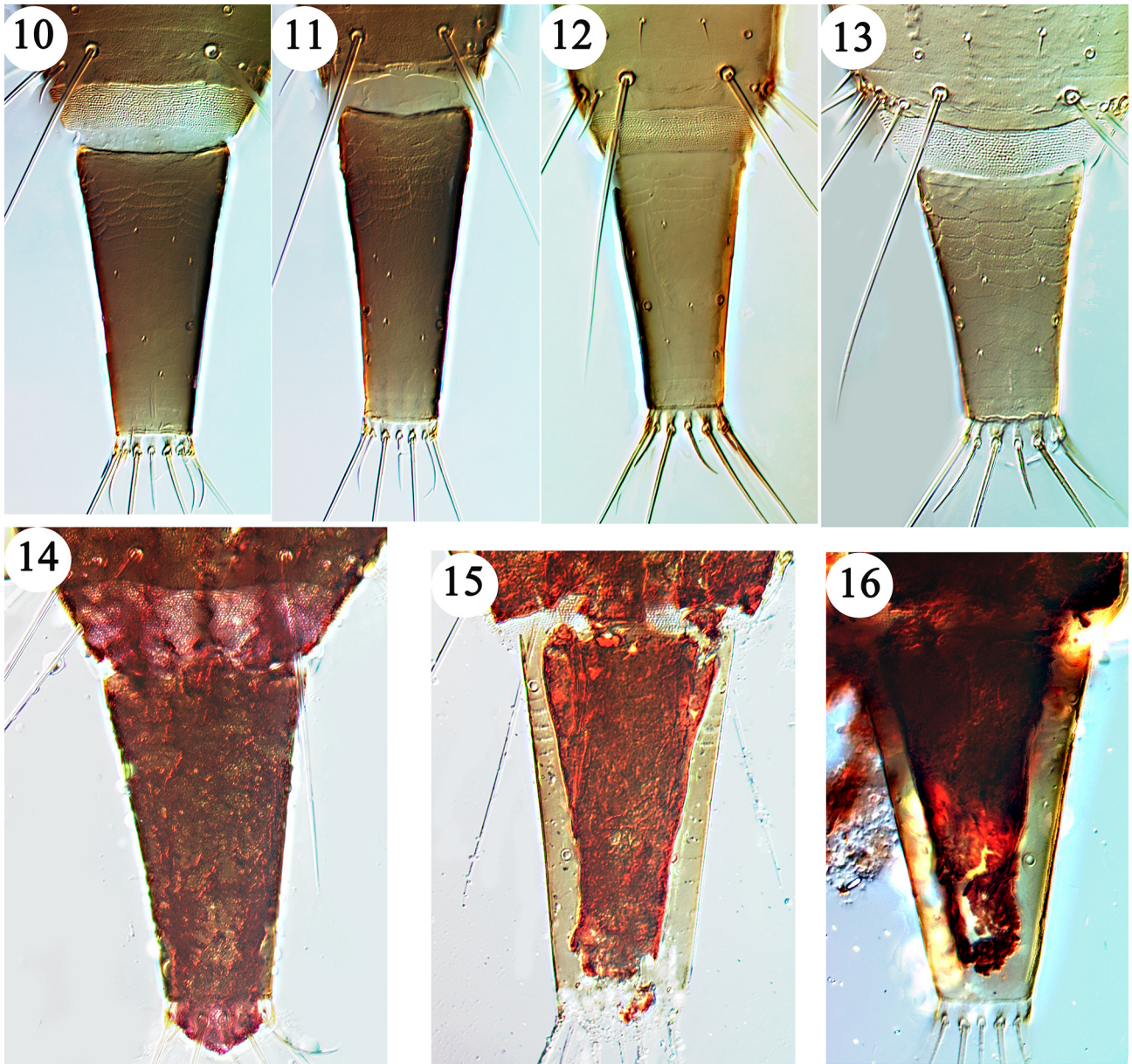
*Leptothrips russelli* Morgan, 1913: 39.

Described from both sexes on *Eriogonum fasciculatum* [Polygonaceae] at Claremont, California, this species is known to breed in the flowers of this plant with no evidence that it is predatory (Wiesenborn 2012). Specimens have also been studied from Nevada and Arizona. Despite sharing with *purpuratus* the presence of a fore tarsal tooth and the absence of duplicated wing cilia, the pronotum of *fasciculatus* has no prominent sculpture lines but has well-developed mid-lateral setae (Fig. 22). Moreover, the sculpture lines on the mesonotum are not closely spaced, but form an almost reticulate pattern (Fig. 28). The fore tarsal tooth of males is considerably larger than that of females.

### ***Leptothrips heliomanes* Hood**

*Leptothrips heliomanes* Hood, 1927a: 202.

Described from an unspecified number of both sexes taken from an unknown plant near Palm Springs, California, a Lectotype was designated for this species by Pitkin (1978: 282). The number of major sense cones on antennal segment IV was stated by Johansen (1987: 78) to be three plus a minor one. However, re-examination of the lectotype and seven specimens bearing the same data has confirmed that all of them bear four *sensilla basiconica* (= major sense cones) on this segment. In May, 2015, *heliomanes* was found in large numbers at Big Morongo Canyon, 50 miles east of Riverside. It was breeding on grasses in association with unidentified mites. Adults collected at the same site but on the leaves of *Prosopis* trees have shorter antennae with only three sense cones on segment IV and possibly represent *papago*. Series of *heliomanes* typically have few or no duplicated cilia on the fore wing, but individuals sometimes have up to 6 cilia on one but not on both fore wings. Moreover, the duplicated cilia on some wings are unusually slender. Samples sometimes include individuals with three major sense cones on segment IV, and if such individuals were collected alone they would be identified as either *papago* or *primigenus*, depending on the presence or absence of duplicated cilia. Despite this, judging from the many specimens in ERMR, it appears that *heliomanes* is a valid species and probably the Western version of the Eastern species *mali*.



**FIGURES 10–16.** *Leptothrips* species of North America – abdominal segment X (tube). (10) *mali* female; (11) *mali* Male; (12) *pini*; (13) *oribates* (*brevicapitis* holotype); (14) *gurdus* holotype; (15) *opimus* holotype; (16) *robustus* holotype.

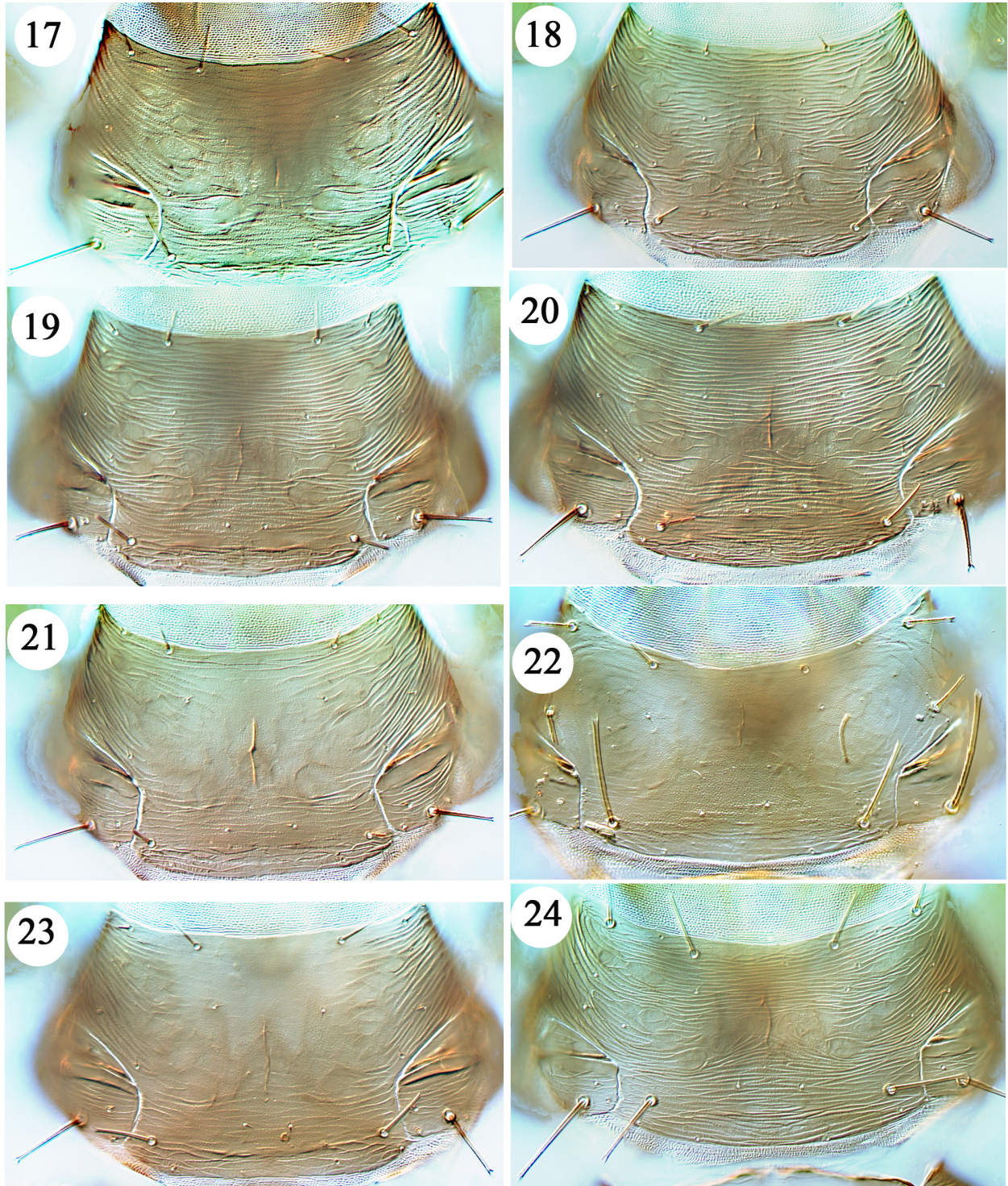
### ***Leptothrips larreae* Hood**

*Leptothrips larreae* Hood, 1939: 207.

Described from Arizona, with paratypes from California, all associated with *Larrea tridentata* [Zygophyllaceae], this species probably feeds on mites within cecidomyiid galls on this plant (Wiesenborn 2015). More than 100 slide mounted specimens from *Larrea* have been studied (from ERMR), mainly collected in California. When the head is truly horizontal, the compound eyes are clearly longer ventrally than dorsally (but see *caveat* above). The postocular setae are short, 20–25 microns in length, scarcely reaching the posterior margin of the eye. The number of duplicated cilia on the fore wing is variable within any given population, with bilateral asymmetry in the number being common. At least 10% of adults have no duplicated cilia on one or both fore wings. Antennal segment IV usually has three sense cones, but a very few specimens have been seen with only two on one antenna. Moreover, the small ancillary sense cone (= *sensillum coeloconicum*) on the external margin of segment IV is present in most



examined specimens, but cannot be seen on one or both antennae of a substantial minority of specimens. Despite this variation, the specimens from *Larrea* consistently have antennal segments III and IV rather short, and antennal segment III with no sense cone. However, not all *Leptothrips* individuals collected from *Larrea* are identifiable as *larreae*. Three specimens from *Larrea* at Banning, California, have a sense cone on antennal segment III, and antennal segments III+IV more than 160 microns long; the two females have four sense cones on segment IV but the male only three, and the number of duplicated cilia varies from 1 to 4 on these three specimens.



**FIGURES 17–24.** *Leptothrips* species of North America – pronotum. (17) *maliaffinis* holotype; (18) *mali*; (19) *papago*; (20) *heliomanes*; (21) *macroocellatus*; (22) *fasciculatus*; (23) *pini*; (24) *purpuratus*.

## ***Leptothrips macroocellatus* Watson**

*Leptothrips aspersus macro-ocellatus* Watson, 1913: 148.

*Leptothrips confusus* Johansen, 1987: 89. **Syn. n.**

The Code of Zoological Nomenclature (<http://www.iczn.org/iczn/index.jsp>) specifies that a hyphen should be deleted from any compound name, except where the first of the two names is a single letter. Watson described this species from an unspecified number of specimens taken from orange leaves at Gainesville, Florida, in January, 1913. Johansen (1987: 93) stated that he had designated a Lectotype of *macroocellatus*, but no such specimen has been found in either USNM or FSAC. The only slides found that bear original data are in FSAC, and these include two larvae and six adults, of which only one has an antenna. Based on these specimens, this species is interpreted as having sculpture lines on the pronotum posteriorly and laterally but not medially (Fig. 21), and in having antennal segment IV with three sense cones. Moreover, the external margin of segment IV bears a small ancillary sense cone (= *sensillum coeloconicum*), although this is not always visible. The compound eyes are large, but the extent to which they are longer ventrally than dorsally depends on the orientation of the head on slide mounted specimens. Samples of this species have been studied (in ERMR) from Florida (Orlando) and South Carolina (Colleton Cty), also (in USNM) from Ft Garland (Colorado). However, a few unidentified specimens mentioned by Mound *et al.* (2016) that were collected from *Jatropha curcas* at Chiapas, Mexico can now be identified as this species, together with 50 specimens representing both sexes collected by Francisco Infante in March and April, 2014, at various sites in the Southern parts of Chiapas State. The species *confusus* was based on a single female from Homestead, Florida (in USNM), and placed in a key between *mali* and *macroocellatus*. This specimen was distinguished from *macroocellatus* because it has the eyes scarcely prolonged ventrally and the major setae rather shorter.

## ***Leptothrips mali* (Fitch)**

*Phloeothrips mali* Fitch, 1855: 806.

*Cryptothrips aspersus* Hinds, 1902: 205. Synonym in Hood, 1914: 162.

*Cryptothrips californicus* Daniel, 1904: 293. Synonym in Hood, 1914: 162.

*Cryptothrips adirondacks* Watson, 1921: 83. Synonym in Hood, 1927b: 112.

*Leptothrips gurdus* Johansen, 1987: 45. **Syn. n.**

*Leptothrips septemtrionalis* Johansen, 1987: 55. **Syn. n.**

*Leptothrips maliaffinis* Johansen, 1987: 61. **Syn. n.**

Johansen distinguished *maliaffinis* and *septemtrionalis* from *mali* on the grounds that specimens of *mali* lack a major sense cone on the external apical margin of antennal segment IV - that is, he claimed that *mali* has only three major sense cones on this segment. However, all available specimens of *mali*, including specimens identified as this species by Johansen himself, have on segment IV four well-developed *sensilla basiconica*, even though one of these is sometimes smaller than the others. Johansen further distinguished *septemtrionalis* from *maliaffinis* on the basis that the former lacks a small accessory sense cone (*sensillum coeloconicum*) on the external margin of antennal segment IV, whereas the latter has such a sense cone. However, although this structure is visible on the right antenna of the holotype female of *maliaffinis* it is not visible on the left antenna, nor on either of the antennae of two available paratypes of *maliaffinis*. Similarly, this small sense cone is not visible on the holotype of *septemtrionalis* nor one male paratype from Virginia, but is clearly visible on the left (but not the right) antenna of a female paratype of *septemtrionalis* from near Blacksburg. There is no evidence from any of the available slides that the small sense cone has been broken off during slide preparation, and the assumption here is therefore that its presence is variable (or that its visibility is variable on slide-mounted specimens). One female from Colorado, identified by Johansen as *californicus*, has this minute sense cone visible on the left antenna but not the right. As discussed above, *gurdus* was described by Johansen as having the tube short and conical, but that wording does not seem appropriate to the tube of either the holotype female (Fig. 14) or the paratype male, and these specimens cannot be distinguished from the common species *mali*. Johansen also placed *mconelli* in the same group with *mali* as having only three major sense cones on antennal segment IV, but placed *californicus* in the group with *maliaffinis* as having four such sense cones. The first of these is here considered a valid species, but the second is

returned to synonymy with *mali*. As interpreted here, *mali* is variable in the colour and length of antennal segments III and IV, with some individuals having these segments largely brown and slender, but others having them shorter and yellow in the basal half. Similar variation in the colour and shape of these antennal segments occurs in the closely related western species, *heliomanes*.

### ***Liothrips mcconelli* Crawford DL**

*Liothrips mcconelli* Crawford DL, 1910: 163.

*Leptothrips primigenus* Johansen, 1987: 72. **Syn. n.**

Although at one time placed as a synonym of *mali*, the presence of only three major sense cones (*sensilla basiconica*) on the fourth antennal segment distinguishes this species. It was collected and described by Crawford from four females and four males taken in Guadalajara, Mexico. From these specimens Johansen (1987) designated a female lectotype (in California Academy of Sciences), and listed many specimens of the species from Mexico and also a few in USA from Utah, Idaho and California. He then described *primigenus* from a single female taken at Yosemite, California, distinguishing it because antennal segment IV of the holotype lacks a small ancillary sense cone (= *sensillum coeloconicum*) on the external surface. This five micron long ancillary sense cone is present on most of the 150 specimens (in ERMR) that are here identified as *mcconelli*, although it is certainly absent on both antennae of a few of them, and *mcconelli* is here interpreted as a common species in California. It is distinguished from *larreae* by the presence of a sense cone on antennal segment III, and the greater length, 130 microns, of antennal segments III+IV, and distinguished from *mali* by the presence on segment IV of three not four major sense cones (*sensilla basiconica*). However, the number of fore wing duplicated cilia is variable amongst the specimens examined. For example, in a series of 14 individuals taken from Sycamore at Riverside (30.vi.1958) the number varies from 0 to 7, two of these specimens have no duplicated cilia on either wing, and one male has antennal segment IV with four sense cones. As indicated above, character state variation amongst the five species, *heliomanes*, *larreae*, *mali*, *mcconelli* and *papago* is very confusing, with the occasional individual intermediate in structure between two or more of these. Specimens identified as *mcconelli* have been studied from Alaska, Arizona, California, Colorado, Texas, and Utah from various plants, particularly tree species in the genera *Acer*, *Alnus*, *Fraxinus*, *Prunus*, and *Quercus*.

### ***Leptothrips occidentalis* Johansen**

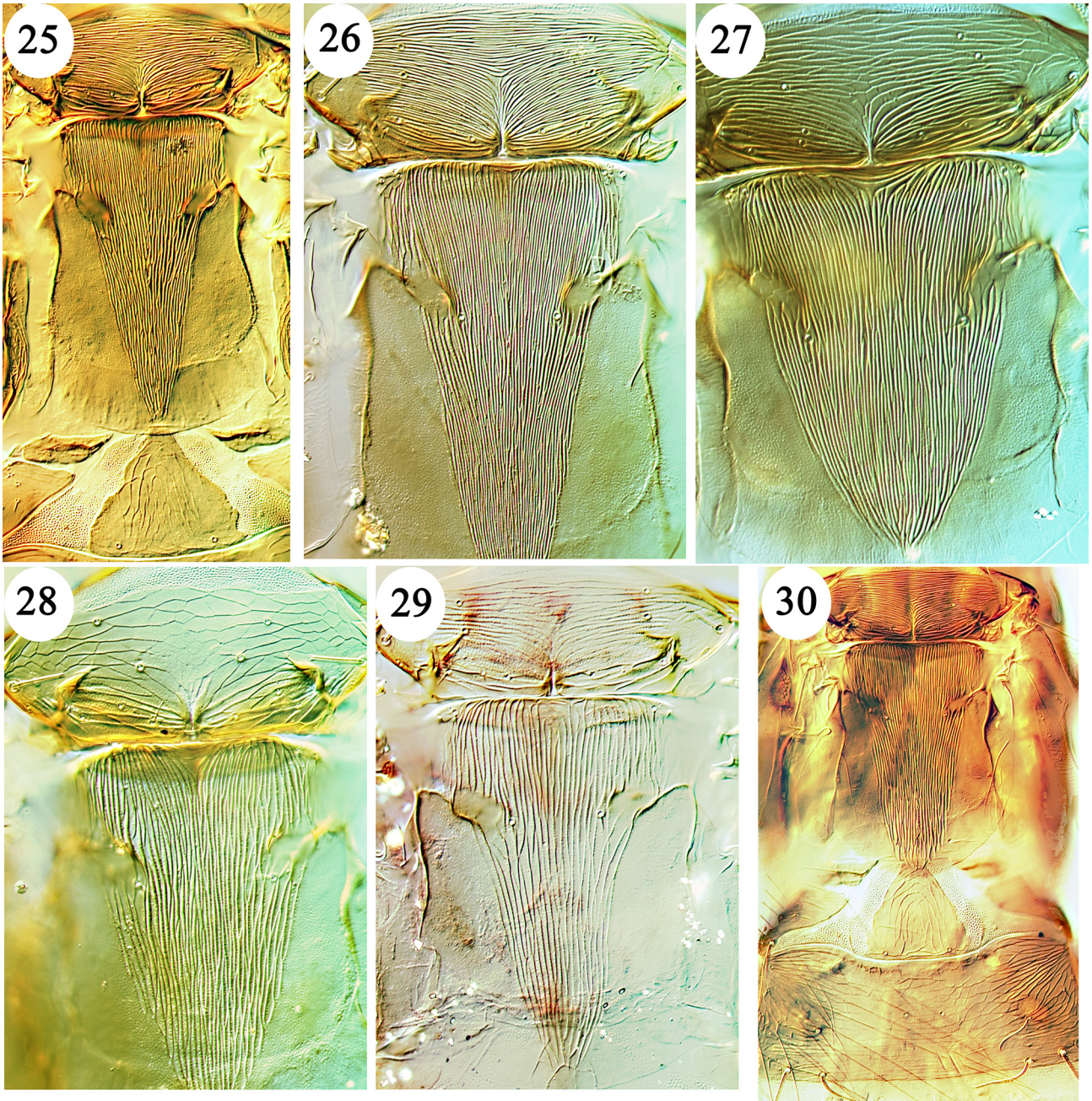
*Leptothrips occidentalis* Johansen, 1987: 59.

This species remains known only from the original specimens: two females and one male collected at Bridgeland, Utah. It is remarkable for the long and deeply retracted maxillary stylets that are close together medially in the head (Fig. 5). Despite this, the species is similar to *heliomanes* in having the pronotum with particularly strong transverse striae, and the fore wing lacking duplicated cilia.

### ***Leptothrips opimus* Johansen**

*Leptothrips opimus* Johansen, 1987: 43.

This species is based on a single female that is labelled "Colorado, Allenspark, Pine, 1950". The specimen is slide-mounted in Clarite, and as a result it is crushed and distorted, with crumpled wings, and the sense cones eroded and faint. The pronotum has strong transverse striae at least on the anterior third, the mesonotum is transversely striate, the basal pores of four major sense cones are visible on antennal segment IV, but the head is too distorted to decide if the eyes are prolonged ventrally. Antennal segment II is asymmetric and presumably aberrant (Fig. 6), and the specimen is possibly a deformed individual of *heliomanes*.



**FIGURES 25–30.** *Leptohiprips* species of North America—metanotum. (25) *mali*; (26) *papago*; (27) *purpuratus*; (28) *fasciculatus*; (29) *oribates* (*brevicapitis* holotype); (30) *occipitalis* holotype.

### ***Leptohiprips oribates* Hood**

*Leptohiprips oribates* Hood, 1939: 205.

*Leptohiprips oregonensis* Hood, 1939:213; Synonymised by O'Neill, 1972: 272.

*Leptohiprips brevicapitis* Johansen, 1987: 52. **Syn. n.**

Described from Colorado, Arizona and New Mexico, with one synonym from Oregon, specimens of this species have also been seen from Nevada and California. It is closely associated with species of *Pinus*, and has been taken several times from immature pine cones. It is distinguished from *pini*, with which it shares this host association, by the presence on antennal segment IV of four sense cones. Both species lack pronotal sculpture and have the fore wings pale at the base, but the available distribution records suggest that they are adapted to rather different

ecological conditions, with *pini* mainly from the Florida area, but *oribates* from the Western states. Johansen described *brevicapitis* from a few specimens associated with *Pinus* from California and Arizona. He stated that these specimens have the eyes prolonged ventrally, in contrast to those of *oribates*. However, the difference between the dorsal and ventral surfaces in the holotype (see Fig. 73 in Johansen, 1987) is trivial, and involves a difference of no more than the diameter of a single ommatidium. The extent to which the eyes are longer ventrally than dorsally in the available specimens of *oribates* is here interpreted as being associated with the orientation of the head in slide-mounted specimens (see discussion above). More than 40 specimens of *oribates* have been studied from various sites in California (in ERMR); two of these were noted to have only three sense cones on segment IV of one antenna (but not on both), and in all of them segment IV lacked a small ancillary sense cone (=sensillum coeloconicum) on the external surface.

### ***Leptothrips papago* Hood**

*Leptothrips papago* Hood, 1939: 209.

*Leptothrips acaciae* Hood, 1939: 211. Synonymised by Johansen, 1987: 79.

*Leptothrips robustus* Johansen, 1987: 47. **Syn. n.**

*Leptothrips arizonensis* Johansen, 1987: 76. **Syn. n.**

This species was based on a female holotype, with three female and one male paratypes, all collected from cottonwood, at Tucson, Arizona. Measurements of the antennae in the four species listed in the synonymy above are remarkably different. The length of antennal segments III+IV is 145 in the holotype of *papago*, whereas the measurements provided by Hood indicate only 107 for the holotype of *acaciae*. The similar measurement for the holotype of *robustus* is 130, and 110 for the holotype of *arizonensis*. No other character state differences have been found that correlate with this variation in antennal segment lengths. A further species in which these segments are unusually short is *larreae*, but in that species antennal segment III lacks a sense cone. Hood described *acaciae* from Wickenburg, Arizona, based on 17 females and one male collected from *Acacia* or *Prosopis*. Johansen described *robustus* from two specimens from Wyoming and one from Colorado, all three being mounted in Clarite. These specimens are thus seriously distorted, with the antennal sense cones almost completely eroded, and the fore wings of the holotype not available. However, one fore wing of the paratype from Wyoming clearly has no duplicated cilia. Johansen distinguished *arizonensis* from *papago* in a key, indicating that the eyes were not prolonged ventrally in the first but prolonged in *papago*. However, the difference in dorsal and ventral lengths of the eyes in the available specimens is largely dependent on how horizontal the head is on a slide-mounted specimen. Johansen placed *robustus* in his Group Obesus, presumably because the tube of the holotype is wide at the base (Fig. 16). However, this specimen is mounted in clarite, and is thus crushed with the tube distorted. Individuals identified here as *papago* have been seen from a wide range of unrelated plants at sites between Utah and California, based on 100 slides in ERMR; the recorded plants include members of the following genera: *Adenostema*, *Ceanothus*, *Chrysothamnus*, *Hymenochloa*, *Purshia* and *Quercus*.

### ***Leptothrips pini* (Watson)**

*Cryptothrips pini* Watson, 1915: 49.

*Zygothrips floridensis* Watson, 1922: 22. Synonymised by Johansen (1987: 97).

Described from Florida, and recorded from Virginia and Maryland, in association with species of *Pinus*, there are specimens in ERMR from Texas, taken on *Pinus taeda* at Smithville, and on *Pinus* sp. at Blossom. The following have also been studied (in USNM): one specimen from Arizona, one from Georgia, five from New York and three from South Carolina. This species shares with *singularis* the presence of only two sense cones on the fourth antennal segment. The pronotum lacks sculptured striae medially but is strongly striate anterolaterally, the fore wing is pale at the base, but the apex of antennal segment III is shaded brown.

## ***Leptothrips purpuratus* (Hood)**

*Haplothrips purpuratus* Hood, 1925: 101.

Described from one female and one male, taken on a species of *Atriplex* at Tempe, Arizona, this species was described as having antennal segments III–VI “bright yellow”. The fore tarsus bears a small tooth on the inner margin, as in *distalis* and *fasciculatus*, and it shares with *distalis* the presence of strong transverse striae on the pronotum but lacks mid-lateral setae. In contrast, *fasciculatus* has a smooth pronotum, and *purpuratus* is unique among the three species of the *distalis* group in lacking a sense cone on antennal segment III. Specimens have been studied from Arizona (Sacaton), California (Tecopa, Thermal, Victorville), New Mexico (Rodeo) and Texas (Ysleta).

## ***Leptothrips singularis* Hood**

*Leptothrips singularis* Hood, 1941: 149.

Described from three females and five males collected at Pine Key, Florida, this species is similar to *pini* but has the pronotum and hind tibiae paler. These two both have only two sense cones on antennal segment IV, but both are known from too few specimens to be sure that this character state is constant. A further species from Florida that is similar in structure and lacks sculpture lines across the pronotum is *cassiae*.

## **Acknowledgements**

We are grateful to the US National Museum of Natural History for providing access to the extensive slide collection that was donated to that museum by J.D. Hood. The holotypes of North American *Leptothrips* species described by Johansen are in the Natural History Museum, London, and were kindly made available on loan in Canberra through the courtesy of Paul Brown. Mark Hoddle generously hand-carried to Canberra from Riverside, California, a loan of almost 1000 microscope slides. These were of specimens slide-mounted by, also mainly collected by, the late Bill Ewart at the Entomology Research Museum, University of California, Riverside.

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