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TWO NEW BASAL-CLADE THYSANOPTERA FROM CALIFORNIA WITH OLD WORLD AFFINITIES

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Abstract.—*Parrellathrips ullmanae* gen. et sp. nov. is described from California in the Fauriellidae, a family previously known only from southern Europe and South Africa. *Heratythrips sauli* gen. et sp. nov. is described from California in the Adiheterothripidae, a family known only from western USA and the Mediterranean and Indian areas. Cladistic analysis of character states in these and related taxa indicates that the present family classification in the lower clades of the Thysanoptera is not strongly supported.

Of the two sub-orders in the insect order Thysanoptera, the Terebrantia includes the most basal elements and was considered by Mound et al. (1980) to comprise seven families. To these seven, however, should be added an eighth, the Melanthripidae, that was previously regarded as a sub-family of the Aeolothripidae (Bhatti, 1990). Amongst these terebrantian families, members of two of the more basal clades, the Adiheterothripidae and the Fauriellidae, show interesting disjunct distributions. The Adiheterothripidae currently comprises two genera, one monobasic in western north America, and the second with four species from several countries between the Mediterranean and India. The Fauriellidae, in contrast, comprises three genera, two monobasic from south eastern Africa and the third with two species from the Mediterranean area. The purpose of this article is to describe from California two new species, each in a new monobasic genus, and one in each of these two families. These taxa not only emphasise the disjunct geographic distributions within these families, they also present considerable problems for the systematic relationships of the basal clades of the order Thysanoptera. Both taxa were found in the collections of the Entomology Research Museum of the University of California at Riverside during a recent visit (by LAM). This Museum includes an extensive collection of Thysanoptera that was developed by William Ewart, who both mounted and distinguished the two thrips discussed here, along with many other undescribed Californian Thysanoptera species.

Little is known of the biology of the thrips in these basal clades. In Adiheterothripidae, species of the Old World genus *Holarthrothrips* apparently breed in the flowers of the date palm (*Phoenix dactylifera*), whereas adults of its west coast New World relative, *Oligothrips*, have usually been found in the flowers of the ericaceous plant manzanita (*Arctostaphylos*). Host-plant relationships in the Fauriellidae are similarly inconclusive and lacking any pattern. The two European species are possibly associated with a grass or some low growing herb, and although both sexes of one of the two South African species were taken from *Elytropappus* (Asteraceae), the only known specimens of the other were taken from an unidentified tree. In contrast,

females and larvae of the new fauriellid from California described below were found in the flowers of a native *Garrya* (Garryaciae).

The new Californian fauriellid described below has a well developed tentorial bridge, although this structure has been lost in the other Fauriellidae. Conversely, the new Californian adiheterothripid lacks a tentorial bridge, whereas other members of this family are reported to retain this structure in its plesiomorphic condition (Mound et al., 1980). Phylogenetic relationships between these and some other thrips taxa in lower clades are therefore explored below.

FAMILY FAURIELLIDAE

This family is not characterised by any single apomorphy, the four genera involved showing a confusing pattern of character states that are intermediate between the states found in several other families. The antennae and their sensoria are similar to those found in the Merothripidae and the Melanthripidae, in that there are nine (rarely eight) antennal segments of which most bear numerous microtrichia, and the third and fourth segments have the sensoria forming a transverse apical band. The new fauriellid species described below retains a complete tentorial bridge as in the Merothripidae, Aeolothripidae and Melanthripidae, although this structure is lost in the previously described species of Fauriellidae as well as in all species of Thripidae. The forewings of fauriellids are slender as in the Thripidae, but cross veins are commonly visible between the costa and the first vein, a plesiomorphic condition that is particularly well developed in the broad wings of members of the Aeolothripidae and Melanthripidae. Finally, the chaetotaxy of the head and also of the seventh abdominal sternite is essentially similar to that found in Thripidae rather than to that found in the more basal taxa.

Within the Fauriellidae, the five known species show an interesting diversity in structure. In the South African *Opisthothrips elytropappi* Hood the posterior abdominal segments and ovipositor are very weakly developed, indicating that this species cannot cut into plant tissue to insert its eggs but must instead deposit them superficially, presumably within the florets of its Asteraceae host. In contrast, the ovipositor and terminal abdominal segments of the new Californian species are exceptionally long. Four of the known species retain the plesiomorphic condition of the maxillary palps with three segments, but the two European species comprising *Ropotamothrips* sometimes have only two maxillary palp segments. These two species are particularly similar to each other, although one has long pronotal posteroangular setae whereas the other has these setae short. The differences between the four recognised genera are summarised in the key below.

KEY TO GENERA OF FAURIELLIDAE

1. Median abdominal tergites each with only two pairs of discal setae, third pair of discal setae arising lateral to pleurotergal sutures (Fig. 5); tergites completely reticulate medially, with transverse reticulations; sternite VII with only 2 pairs of major setae, the lateral pair greatly reduced (Fig. 10); forewing with 2 cross veins clearly visible between costa and first vein; forewing posterior fringe cilia distinctly undulating; maxillary palps sometimes with only 2 segments . . . . . *Ropotamothrips*

– Median abdominal tergites each with three pairs of discal setae, third pair of discal

setae arising mesad of pleurotergal sutures (Fig. 3); tergites with median reticulation weak or almost absent; sternite VII with 3 pairs of setae (Figs. 11–13); forewing with cross veins weak or absent between costa and first vein; forewing posterior fringe cilia straight or almost straight; maxillary palps with 3 segments 2

2. Prosternal ferna fused medially (Fig. 7); head with tentorial bridge complete medially; forewing second vein with 8 to 10 setae; sternite VII median setae (B1) at margin, setae B2 and B3 arising in front of posterior margin (Fig. 13); antennal segment III almost 4.0 times as long as maximum width (Fig. 9) . . . . . *Parrellathrips*

– Prosternal ferna separated (Fig. 6); head with tentorial bridge not visible; forewing second vein with 3 to 5 setae; sternite VII setae arranged differently; antennal segment III 2.0 times as long as wide or shorter 3

3. Antennae with 8 segments; sternite VII sclerotised area reduced to a narrow transverse band bearing three pairs of setae close together (Fig. 11); metanotum with neither setae nor pores near posterior margin; ovipositor very weak; forewing second vein with 3 setae . . . . . *Opisthothrips*

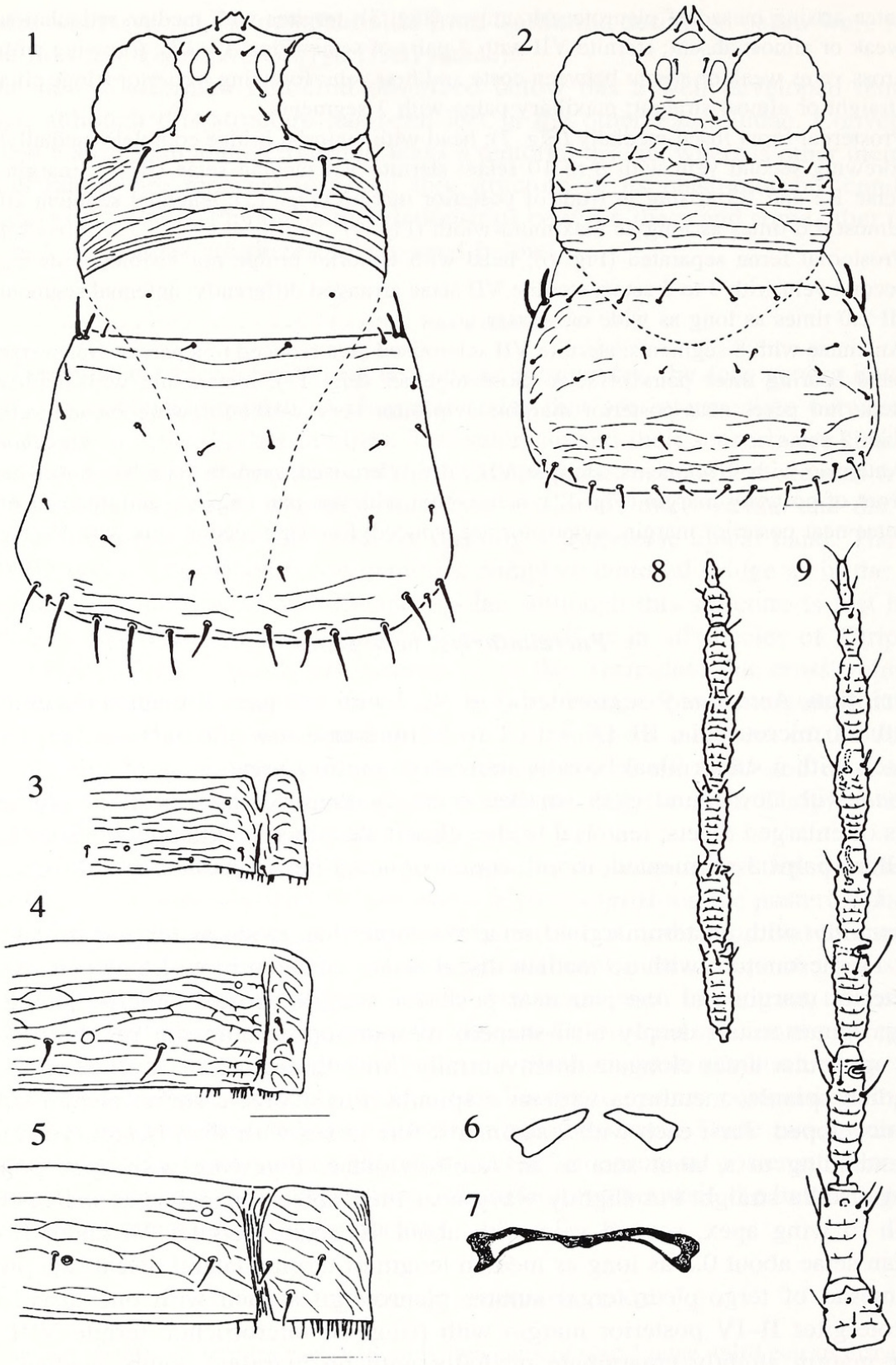
– Antennae with 9 segments; sternite VII fully sclerotised, median setae arise well in front of posterior margin (Fig. 12); metanotum with one pair of pores and one pair of setae near posterior margin; ovipositor not reduced; forewing second vein with 5 setae . . . . . *Fauriella*

Parrellathrips, new genus

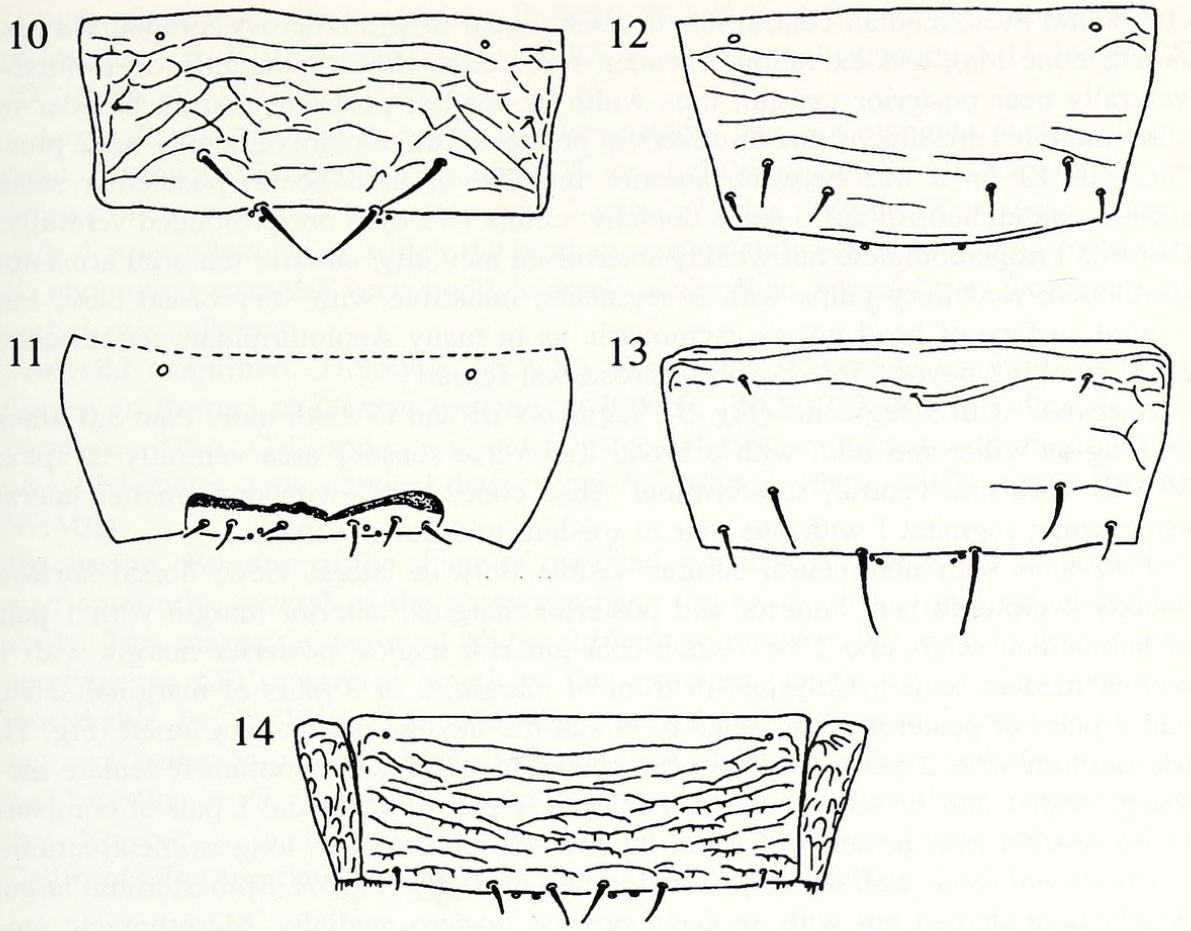
Description. *Antennae* 9-segmented (Fig. 9); I with one pair of median dorsal setae, II without microtrichia, III–IX with 1 to 5 transverse rows of microtrichia, III and IV each with a subterminal broadly transverse sensory area.

Head with compound eyes smaller ventrally than dorsally, without pigmented facets or enlarged facets; tentorial bridge clearly developed, although weak medially; maxillary palps 3-segmented; mouth cone extending between and beyond fore coxae (Fig. 1).

Pronotum with posteromarginal setae not more than twice as long as discal setae (Fig. 1); mesonotum with no median discal setae; metanotum with one pair of setae at anterior margin and one pair near posterior margin; prosternal ferna joined medially; spinasternum deeply boat-shaped; mesopre-episternum not fused; mesothoracic spiracular areas elongate dorsoventrally. Mesothoracic furca well developed as a median spinula, metafurca without a spinula. Metathoracic sterno-pleural sutures well developed. Tarsi each with 2 segments; fore tarsus with sharply recurved hamus not extending to a stout seta as in Aeolothripidae. Forewing with apex pointed; posterior cilia straight but slightly wavy near their apices; veinal setae increasing in length to wing apex, second vein with about 10 setae. Tergites VI and VII with median setae about 0.5 as long as median length of tergite, lateral discal seta present just mesad of tergo-pleurotergal suture; pleurotergites each with one discal seta, pleurotergites II–IV posterior margin with fringe of microtrichia; tergite VIII posterior margin slightly emarginate medially with no marginal comb, median setae extending beyond posterior margin; tergite X longer than median length of tergite VIII. Sternites with 3 pairs of primary (marginal) setae, no discal setae; sternite VII with B2 and B3 arising sub-marginally, B1 arising at margin, adjoining bases of setae B1 are two pairs of minute pores presumably representing bases of vestigial setae of sternite VIII (Fig. 13). Ovipositor long and well developed, extending be-



Figs. 1–9. 1. Head and pronotum, *Parrellathrips ullmanae*. 2. Head and pronotum, *Heratythrips sauli*. 3. Tergite IV, *Opisthothrips elytropappi*. 4. Tergite VI, *Heratythrips sauli*. 5. Tergite IV, *Ropotamothrips*. 6. Prosternal ferna, *Fauriella natalensis*. 7. Prosternal ferna, *Parrellathrips ullmanae*. 8. Antennal segments III-IX, *Heratythrips sauli*. 9. Antenna, *Parrellathrips ullmanae*.



Figs. 10–14. Sternite VII. 10. *Ropotamothrips buresi*. 11. *Opisthothrips elytropappi*. 12. *Fauriella natalensis*. 13. *Parrellathrips ullmanae*. 14. *Heratythrips sauli*.

yond apex of abdomen, weakly curving downward at apex. Type-species *Parrellathrips ullmanae* sp.n.

Discussion. This new genus and species is named in recognition of the outstanding work on the biology of pest Thysanoptera by the research teams at the University of California at Davis led by Michael Parrella and Diane Ullman. The genus is evidently closely related to other members of the family Fauriellidae, but is remarkable for the retention of the tentorial bridge in the head. Relationships to the other taxa in this family are discussed further below.

Parrellathrips ullmanae, new species

Description. *Macropterous female.*

Color: Body, legs and antennae mainly medium brown; all tarsi yellow; antennal segment II yellow at apex, III yellowish washed with pale brown, IV slightly paler than V–IX; fore tibiae yellow but variably washed with brown; major setae not dark; forewing lightly shaded, but with extreme apex dark.

Structure: Head slightly produced medially between antennal bases (Fig. 1), this extension deeply cleft medially; median dorsal length of head less than width across

compound eyes, median ventral length about equal to width across compound eyes, mouth cone long and extending between fore coxae [head apparently deep dorso-ventrally near posterior margin, thus width of head at posterior margin broader in slide-mounted specimens due to coverslip pressure]; three pairs of ocellar setae present, pair III on a line between anterior margins of hind ocelli; postocular setae forming an arched row of 5 setae dorsally; compound eyes not prolonged ventrally; tentorial bridge complete but weakly sclerotised medially, anterior tentorial arms not developed; maxillary palps with 3 segments; mandible with very broad base, but ventral surface of head not as asymmetric as in many Aeolothripidae; mouth cone long, reaching beyond fore coxae to prosternal ferna.

Antennae with 9 segments (Fig. 9), segments III and IV both more than 3.0 times as long as wide, and both with a broad transverse sensory area ventrally at apex; V–VIII with one ventral, sub-terminal sense cone, V–VI with one smaller lateral sense cone; segment I with one pair of median mid-dorsal setae.

Pronotum with notopleural sutures visible only in lateral view; dorsal surface weakly sculptured near anterior and posterior margins; anterior margin with 1 pair of submedian setae, and 2 or 3 setae near anterior angles; posterior margin with 1 pair of median setae arising just in front of margin, 2 or 3 pairs of marginal setae, and 3 pairs of posteroangular setae of which the median pair is very small (Fig. 1). Mesonotum with 2 pairs of setae near posterior margin. Metanotum reticulate medially, with 1 pair of setae at anterior margin, 1 pair of setae and 1 pair of campaniform sensilla near posterior margin; metascutellum almost as long as metascutum.

Prosternal ferna well developed and joined medially (Fig. 7). Spinasternum large, deeply boat shaped but with an acute process postero-medially. Mesothoracic pre-episternum variable, usually completely distinct but sometimes weakly fused ventro-medially.

Tibiae with 1 or 2 moderately developed stout apical setae. Forewing not broad, tapering to a point; cross veins weakly developed; clavus with 5 marginal setae; first vein with 3 setae and 1 campaniform sensillum near base, then 3 setae before cross vein, followed by about 9 setae to apex; second vein with 1 seta basal to cross vein, then about 9 setae in distal row to apex; these setae increasingly longer toward wing apex; fringe cilia straight but with extreme apices weakly undulating.

Abdominal tergite I with about 4 transverse lines of sculpture, 1 pair of campaniform sensilla medially and 1 pair of minute setae laterally; tergites II–VIII with 2 pairs of discal setae, median pair mesad of median campaniform sensilla, with almost no sculpture and no microtrichia; tergite X elongate, with median split extending 0.3 from posterior margin, without paired trichobothria. Ovipositor valves weakly curving downward, extending slightly beyond abdominal apex. Sternites III–VI each with 3 pairs of marginal setae, II usually with only 2 pairs and with 3 pairs of small setae near anterior margin; sternite VII (Fig. 13) B1 setae long and arising at margin, B2 setae far anterior of margin, B3 slightly anterior of margin; two pairs of minute pores close to base of B1 setae probably represent bases of vestigial setae of sternite VIII.

Measurements (holotype female and smallest paratype, in microns): Body length 1750 (1500). Head, dorsal length 110; ventral length of head capsule 125; total ventral length to apex of mouth cone 290; width of head across compound eyes 130. Pronotum, length 150; maximum width 210; longest posterior seta 30. Forewing, length 1100; median width 70; length of basal and distal setae on first vein 30, 60.

Length of median setae on tergites II, VIII, IX and X–8, 35, 70, 30; median length of tergites VII, VIII, IX and X–85, 65, 85, 120. Antennal segments I–IX length 25, 50, 75, 60, 50, 50, 45, 30, 25.

Larva II: Head small in relation to large body, legs not elongate. Antennal segment V subequal in length to segment IV or slightly longer, III–VII each with 3 or 4 rows of microtrichia. Pronotum with 7 pairs of setae. Tergite IX posterior margin with 4 stout tubercles of which the median pair extends beyond midpoint of tergite X; abdominal spiracles very small, scarcely wider than a setal base. Sternites each with 3 pairs of setae.

Material examined. Holotype, ♀, USA, California, Riverside County, Mountain Center, in flowers of *Garrya vealchii* at 4000 ft., 20.1.1983, R. K. Velten, (CAS). Paratypes: USA, California: 2 ♀ and 6 instar II larvae, collected with the holotype; also 17 females with identical data except 6.1.1983, J. Pinto, (UCR; CAS; USNM; NHML).

Discussion. Because of the shape of the head, which is deeper at the posterior part than anteriorly, several of the paratypes have the head crushed and orientated laterally. This makes the tentorial bridge difficult to observe, but even in the smallest paratype the full transverse length of this structure can be traced. The species is remarkable for its large size, with the antennae, ovipositor and tenth abdominal segment being particularly long. The presence of larvae indicates that the species was breeding on *Garrya vealchii*, and the stout posterior spines of the larvae suggest that they pupate in the soil. Members of the Garryaceae are found particularly in California, but the family extends to Mexico and the Caribbean.

FAMILY ADIHETEROTHRIPIDAE

The genus *Adiheterothrips* Ramakrishna is a junior synonym of *Holarthrothrips* Bagnall, but is available and has priority as the root for the family name. All members of this family have a curious conical sensorium on the third and fourth antennal segments. A similar sensorium is known from the antennae of the members of the Stenurothripidae, a family known only from fossils (Schliephake, 1990). Other character states are varied between the three genera recognised here, and these can be distinguished by means of the following key.

KEY TO GENERA OF ADIHETEROTHRIPIDAE

1. Forewing second vein with no setae on basal stem; sternites with 3 pairs of posteromarginal setae scarcely twice as long as marginal microtrichia; fore tarsus without a recurved ventral hamus; head and pronotum lacking setae longer than median length of one posterior ocellus (Fig. 2); tentorial bridge not developed . . . . . *Heratythrips*
– Forewing second vein with 2 or more setae basal to cross vein between first and second veins; sternites with posteromarginal setae prominent, usually 4 pairs present; fore tarsus with well-developed recurved ventral hamus; head or pronotum usually with at least one pair of setae twice as long as a posterior ocellus; tentorial bridge usually present 2
2. Sternite VII usually with 4 pairs of setae, one pair arising on posterior margin medially, one pair arising close to these but in front of margin, 2 pairs arising laterally far in front of posterior margin; sternites IV–VI without discal setae; tergites VII and VIII

without any posteromarginal microtrichia; metanotal sculpture reticulate or elongate reticulate, without microtrichia ..... *Oligothrips*

– Sternite VII with 4 (or 3) pairs of posteromarginal setae and about 3 pairs of discal setae laterally; sternites IV–VII often with discal setae laterally; tergites VII and VIII with complete posteromarginal comb of microtrichia; metanotum with concentric rings of sculptured lines bearing numerous microtrichia ..... *Holarthrothrips*

Heratythrips, new genus

Description. *Antennae* 9-segmented (Fig. 8); I with one pair of median dorsal setae, II–IX each with up to 8 transverse rows of microtrichia, III and IV each with a small conical sense cone at apical external margin.

Head with eyes equal in size dorsally and ventrally, with no pigmented nor enlarged facets; tentorial bridge not visible; maxillary palps 3-segmented; mouth cone not reaching fore coxae; dorsal surface without long setae, 3 pairs of ocellar setae present, postocular setae form an irregular row of about 5 setae dorsally.

Pronotum with posteromarginal setae not more than twice as long as discal setae; mesonotum with no median discal setae; metanotum with one pair of setae at anterior margin and one pair near posterior margin; prosternal ferna slender but joined medially; spinasternum deeply boat-shaped; mesopre-episternum not fused; mesothoracic spiracular areas elongate dorsoventrally. Mesothoracic furca well developed as a median spinula, metafurca without a spinula. Metathoracic sterno-pleural sutures well developed. Tarsi each with 2 segments; fore tarsus without a recurved hamus. Forewing with apex pointed; posterior cilia straight but slightly wavy near their apices; veinal setae very small, gradually increasing in length to wing apex, second vein with about 5 setae.

Tergites VI and VII with transverse lines of sculpture medially, each tergite with fine microtrichia on the lines of sculpture laterally, and posterior margins with a comb of microtrichia laterally on II–VII; median setae less than 0.3 times as long as median length of tergite, lateral discal seta present just mesad of tergo-pleurotergal suture (Fig. 4); pleurotergites II–VII each with one discal seta and a posteromarginal fringe of microtrichia; tergite VIII without a marginal comb, median setae not extending to posterior margin; tergite X not longer than median length of tergite IX. Sternites IV–VII with 3 pairs of marginal setae but no discal setae (Fig. 14); ovipositor well developed and curving downward at apex. Type-species *Heratythrips sauli* sp.n.

Discussion. This new genus and species is named in recognition of the support given by John Heraty and Saul Frommer to the senior author's studies on thrips whilst visiting the magnificent collections developed by Bill Ewart at the University of California, Riverside. Related to *Oligothrips* and *Holarthrothrips* by the presence of a distinct but small conical sense cone on the third and fourth antennal segments, it is distinguished in the key to genera above. As in *Holarthrothrips*, it retains the plesiomorphic chaetotaxy of sternite VII with three pairs of setae at the posterior margin (Fig. 14), and the tergites have a marginal fringe of microtrichia laterally (Fig. 4). But the basal stem of the second vein of the forewing does not bear any setae, the metanotum lacks microtrichia, and the tentorial bridge is not visible. The relationships of this genus are discussed further below.

Heratythrips sauli, new species

Description. *Macropterous female.*

Color: Body mainly brownish yellow, tibiae darker, antennal segments II–IX brown; forewings pale, but with extreme apex dark.

Structure: Head slightly produced medially between antennal bases (Fig. 2), this extension deeply cleft medially; median dorsal length of head less than width across cheeks; three pairs of ocellar setae present, pair III on a line between anterior margins of hind ocelli; postocular setae forming an irregular row of 5 setae dorsally; compound eyes not prolonged ventrally; tentorial bridge not visible; maxillary palps with 3 segments; mandible with broad base; mouth cone short and not reaching fore coxae.

Antennae with 9 segments (Fig. 8), segments III and IV both about 2.5 times as long as wide, and both with a small oval bud-like sense cone at apex, V–VII each with a slender sense cone near apex; segment I with one pair of median mid-dorsal setae.

Pronotum without long setae, dorsal surface very weakly sculptured near anterior and posterior margins; anterior margin with 1 pair of submedian setae, and 2 or 3 longer setae near anterior angles; posterior margin with about 6 pairs of setae of which 2 or 3 pairs of posteroangulars are longest (Fig. 2). Mesonotum with 2 pairs of setae near posterior margin. Metanotum reticulate medially, with 1 pair of setae at anterior margin, 1 pair of setae and 1 pair of campaniform sensilla near posterior margin; metascutellum two-thirds as long as metascutum. Prosternal ferna slender but joined medially. Spinasternum large, deeply boat-shaped. Mesothoracic pre-episternum apparently weakly fused ventro-medially.

Hind tibiae with 1 or 2 moderately developed stout apical setae. Forewing not broad, tapering to a point; cross veins weakly developed; clavus with 5 marginal setae; first vein with 3 setae and 1 campaniform sensillum near base, then 3 setae before cross vein, followed by 5 to 7 setae to apex; second vein with 1 seta basal to cross vein, then 5 or 6 setae distally to apex; these setae are scarcely twice as long as the veinal microtrichia near wing base, increasingly longer toward the wing apex; fringe cilia straight with extreme apices faintly wavy. Abdominal tergite I with about 4 faint lines of sculpture, 1 pair of campaniform sensilla medially and 1 pair of minute setae laterally; tergites II–VII with 3 pairs of discal setae, median pair mesad of median campaniform sensilla, with several lines of sculpture medially, posterolateral margins with a fringe of microtrichia (Fig. 4); tergite VIII without marginal microtrichia and median setae extending just beyond posterior margin; tergite X not elongate, with median split extending 0.3 from posterior margin, without paired trichobothria. Ovipositor valves down-curved, not extending beyond abdominal apex. Sternites III–VII each with 3 pairs of marginal setae; sternite II with 2 pairs of marginal setae and 3 pairs of small setae near anterior margin; sternite VII with two pairs of minute pores close to bases of median setae probably representing bases of vestigial setae of sternite VIII (Fig. 14).

Measurements (holotype female in microns): Body length 1250. Head, length 100; width 145. Pronotum, length 100; width 170; longest posterior seta 15. Forewing, length 800; median width 60; length of basal and distal setae on first vein 10, 15,. Length of median setae on tergites II, VIII, IX and X 10, 15, 50, 50; median length

of tergites VII–X 75, 75, 60, 60. Antennal segments I–IX length 13, 35, 40, 40, 38, 40, 35, 25, 13.

Material examined. Holotype, female, USA, California, San Bernadino County, Providence Mts, 6 miles S.E. Kelso Dune, ex *Coleogyne*, 27.4.1968, W. Ewart (CAS). Paratype: USA, California: 1 female collected with the holotype (UCR).

Discussion. Although two females were taken together, this cannot be taken as evidence that the host plant of the species is *Coleogyne* nor even any other member of the family Rosaceae.

Holarthrothrips Bagnall

Bhatti (1986) included four species in this genus. Curiously, all four of these species have been taken from the inflorescences of *Phoenix dactylifera*, the date palm, but the differences between them seem unlikely to represent population variation within a single species. For example, the Indian species *H. jambudvipae* lacks any elongate pronotal setae unlike the other three species; *H. josephi* from Iraq has a postero-marginal comb of microtrichia on most abdominal tergites whereas this is found only on tergites VII and VIII in the other species; *H. tenuicornis* and *H. jambudvipae* both apparently lack sternal discal setae, and both have paired mesothoracic sternopleural sutures, in contrast to the other two species. This variation in structural detail, despite the general uniformity of body form within the genus, coupled with the common host plant, is a remarkable example of intra-generic radiation. The structure of the abdomen is particularly similar to that of species of the family Heterothripidae.

Oligothrips Moulton

Only one species has been described in this genus, *O. oreios* Moulton (1933), and material has been studied from many parts of California, from Shasta and Nevada Counties in the north to Riverside and San Bernardino Counties in the south. In addition, one female has been studied from Utah, Washington County, one female and one male from an unspecified locality in Oregon, and a series of both sexes from *Actostaphylos* flowers at an unspecified locality in Arizona. Three females from Grass Valley, Nevada County, the type locality in California, have the head longer than wide, the ocellar setae sufficiently long to extend beyond the posterior margin of the hind ocelli, the anteromedian pair of pronotal discal setae more than 2.0 times as long as the minor discal setae, and the metanotal sculpture with elongate, linear reticulation. Unfortunately, the holotype itself is so poorly prepared that the condition of the first three characters cannot be confirmed, although the metanotal sculpture agrees with the above description. Specimens studied from most other Californian localities have the metanotal sculpture similar, but the ocellar setae are shorter and do not extend to the posterior margin of the hind ocelli, and the anteromedian pronotal discal setae are scarcely 1.5 times as long as the minor discal setae. In contrast, the single female from Utah has the ocellar setae no longer than the length of one ocellus, the pronotal discal setae are all small and equal in size, and the metanotal reticulation is almost equiangular. The specimens from Arizona are intermediate in structure between those from California and the female from Utah. However, the male and female specimens from Oregon are smaller in size with the head shorter

Table 1. Data set for nine genera of Thysanoptera.

Damerothrips	00001000001000000000
Opisthothrips	11000011100000001011
Parrellathrips	00000100100000001010
Ropotamothrips	10010011101100000110
Oligothrips	00200100010002010010
Holarthrothrips	00200100010002020010
Heratythrips	10201100110001000010
Heterothrips	10100100010012121010
Fauriella	10000100100000001010

and broader, all the setae distinctly shorter, and the metanotum reticulate. In all of the available Californian specimens the sternites bear numerous microtrichia, whereas the females from Arizona, Utah and Oregon lack microtrichia on the sternites, although these structures are present on the male from Oregon. It is possible that the available Californian specimens represent one species, *O. oreios* Moulton, but that the specimens from Arizona, Utah and Oregon represent further undescribed species. The most curious difference between these samples is that a tentorial bridge is visible in the specimens from Grass Valley, and is dark brown and very obvious in the Arizona specimens, but is not visible in the other specimens, suggesting that the sclerotisation of this structure is variable between populations.

SYSTEMATIC RELATIONSHIPS

As indicated in the Introduction, both of the new taxa described here differ in at least one important character state from other members of the two families in which they are placed. Moreover, the family Fauriellidae is not defined on any single apomorphy, but comprises a group of species in which several character states are intermediate between those found in other recognised families. Even the second instar larvae of *Parrellathrips ullmanae* that are described above, the only larvae known for any Fauriellidae, have no apomorphies by which they can be distinguished from larvae of related families. In the key to larvae by Heming (1991) the *Parrellathrips* larvae run to the family Aeolothripidae but have shorter antennae than members of that family.

Because of the difficulties outlined above, a data matrix of character states was compiled for all genera of the Fauriellidae and Adiheterothripidae together with *Heterothrips* of the Heterothripidae, and including *Damerothrips* of the Merothripidae as out-group (Tables 1, 2). This was then analysed under parsimony using Hennig86 (Farris, 1988) operating under the Microsoft Windows shell Tree Gardener 1.0 (Ramos, 1996). These analyses produced results that are significant to the recognition of the families Adiheterothripidae and Fauriellidae, and also to the relationship between these groups and the Heterothripidae.

The Hennig86 option used, an exact tree search (option ie) with all characters additive, produced three trees (length 32, CI .625). The single tree retained after successive weighting (Fig. 15) supported neither Fauriellidae nor Adiheterothripidae as a clade. Various other weight and character type options were tried, but almost

Table 2. Character states for nine genera of Thysanoptera.

Tentorial bridge: 0—complete; 1—absent.
Number of antennal segments: 0—9; 1—<9.
Sensoria on antennal segments III and IV: 0—transverse and simple; 1—transverse and porous; 2—emergent and conical.
Maxillary palp segments: 0—3 present; 1—2 present.
Fore tarsal recurved hamus: 0—present; 1—absent.
Prosternal ferna: 0—separate; 1—fused medially.
Metanotal campaniform sensilla: 0—1 pair present near posterior; 1—absent.
Metanotal posterior setal pair: 0—present; 1—absent.
Forewing second vein basal to cross vein: 0—with setae; 1—without setae.
Forewing cross veins between costa and first vein: 0—2 visible; 1—0 visible.
Forewing posterior fringe cilia: 0—straight; 1—undulating.
Median abdominal tergites with: 0—2 discal setae laterally; 1—1 discal seta laterally.
Tergite IV median setae: 0—wider apart than their length; 1—long and close together.
Tergite IV with marginal comb posterolaterally: 0—absent; 1—present but short; 2—present long and slender.
Pleurotergal sutures: 0—present; 1—absent.
Median sternites: 0—with no posteromarginal fringe; 1—with short posteromarginal fringe; 2—with long fringe.
Sternite VII marginal setae: 0—arising at margin; 1—one or more pairs in front of margin.
Sternite VII setae: 0—3 or more pairs; 1—2 pairs.
Sternite VIII: 0—present as paired lobes; 1—absent.
Ovipositor valves: 0—normal; 1—greatly reduced.

all similarly failed to find support for either family. In Fauriellidae, *Opisthothrips* and *Ropotamothrips* consistently were placed together, although at bootstrap score below the conventional critical value. *Parrellathrips* and *Fauriella* mostly were placed as a sister-group to a clade comprising Adiheterothripidae plus Heterothripidae. Bootstrap scores in the original analysis were 0.63 for *Opisthothrips* + *Ropotamothrips*, and 0.72 for Adiheterothripidae + Heterothripidae. *Heterothrips* was placed as sister to *Holarthrothrips* in some trees, but as sister to *Holarthrothrips* plus *Oligothrips* in others.

The position on the tree of *Heterothrips* relative to the three genera comprising the Adiheterothripidae is particularly interesting. In effect, the Adiheterothripidae is defined on just one character—the presence of a conical sensorium on antennal segments three and four. However, this character state is also found in several closely related Baltic Amber fossils placed in the fossil family Stenurothripidae (see Schliephake, 1990); it is thus plesiotypic within this lineage and may indicate an ancient and previously widespread group. In contrast, the Heterothripidae have the sensoria on antennal segments three and four forming a circumpolar porous band, and members of this family are restricted to the New World. Homoplasy between the antennal sensorial structure of the Adiheterothripidae and Heterothripidae is inconceivable, but the possibility exists that the Heterothripidae is a relatively new lineage that developed only after the separation of the New World continent from the Old World. In contrast, Mound et al. (1980) placed this family as the sister group of the Fauriellidae, a suggestion for which there is now little support.

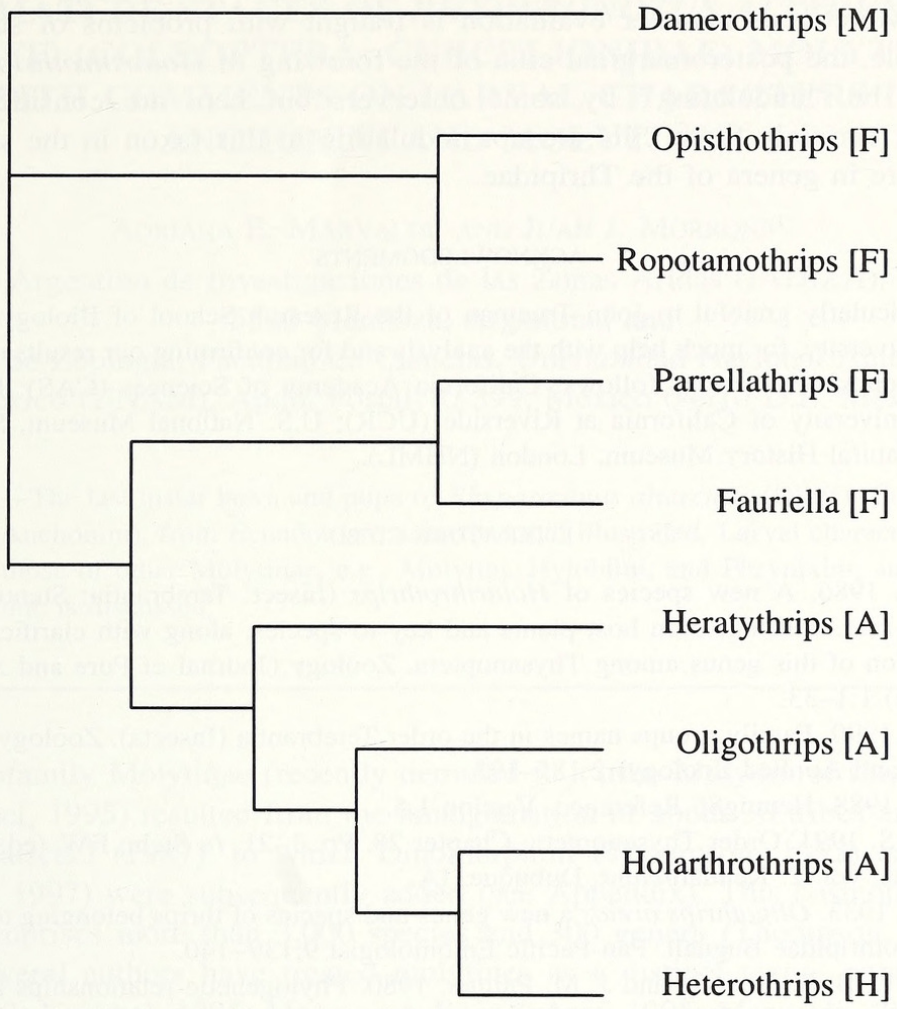


Fig. 15. Computed relationships between nine genera of Thysanoptera (Hennig86 "ie" with successive weighting) [A] = Adiheterothripidae; [F] = Fauriellidae]; [H] = Heterothripidae; [M] = Merothripidae.

Relationships between the four genera now placed in the Fauriellidae are as unresolved as the significance of the family itself. *Opisthothrips* from southern Africa and *Ropotamothrips* from southern Europe are associated on the tree (Fig. 15) only through 'loss apomorphies' on the metanotum. Similarly, *Parrellathrips* from California is associated with *Fauriella* from southern Africa only by the chaetotaxy of sternite seven which is probably due to homoplasy.

The problem with defining lineages within the Thysanoptera arises partly from the high levels of homoplasy exhibited in many character states, but also from the frequency that 'loss apomorphies' are employed to define groups in this order of insects. For example, presence of a tentorial bridge is a plesiomorphy, but loss of this structure could well arise through the action of non-homologous mutations, and evidence given above suggests that this structure is variably developed within the genus *Oligothrips* and possibly within species of that genus. Similar problems arise with loss of veins in the forewings, or loss of setae on these veins, or the loss of setae on the posterior half of the metanotum. Similarly, homoplasy is clearly involved in the number and placement of setae on the posterior margin and the discal area of the

sternites. Moreover, character evaluation is fraught with problems of subjectivity. For example, the posteromarginal cilia of the forewing of *Holarthrothrips* are considered to be "undulating" by some observers but here are considered to be "straight"; certainly these cilia are not undulating in this taxon in the same sense that they are in genera of the Thripidae.

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