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SPIRACULAR STRUCTURE DIFFERS AMONG ADULT AND LARVAL PHLAEOTHRIPIDS (THYSANOPTERA: PHLAEOTHRIPIDAE) RECORDED IN CALIFORNIA DESERTS

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ABSTRACT

Spiracles on Thysanoptera have a diverse and complex structure suggesting they function as plastrons and enable respiration during submergence from rainfall or flooding. I examined the mesothoracic, metathoracic, and first-abdominal spiracles on adult males and females of 4 species of Phlaeothripidae that inhabit the Mojave and Sonoran Deserts. Spiracles contained open pores surrounded by a network of cuticle. I observed 2 classes of spiracle structure, termed compound and simple. Most pores on compound spiracles contained a central spot of cuticle. Most pores on simple spiracles lacked a cuticular spot. Compound spiracles were observed on *Leptothrips larreae* Hood. Simple spiracles were observed on *Liothrips xanthocerus* Hood, *Leptothrips fasciculatus* (Crawford), and the wing-dimorphic *Bagnalliella mojave* Hood. First- and second-instar larvae of *L. larreae* and *L. fasciculatus* supported the same class of spiracles as adults. Metathoracic spiracles on macropterous *B. mojave* females were slightly larger than those on brachypterous females. A live *L. larreae* adult submerged in water, and illuminated obliquely from above, reflected light from its pterothoracic spiracles, indicating that they trap air and likely function as plastrons. Pterothoracic spiracles were also examined on museum slides of adult females of 8 additional, phlaeothripid species recorded in California at desert localities or on desert plants. Four species have compound spiracles, and 4 species have simple spiracles. These 2 classes of spiracles were independent of body size. Spiracle class was weakly, and non-significantly, dependent on brachyptery in either sex. All 4 species with brachypterous males or females produce adult females with simple spiracles. Of the 8 species with only macropters, 5 species support compound spiracles, and 3 species support simple spiracles. Simple spiracles may be more common on desert Phlaeothripidae that produce brachypters and live in enclosed microhabitats, providing more protection from submergence in rainfall.

Key Words: Insecta, Tubulifera, plastrons, wing dimorphism, photomicrographs

RESUMEN

Los espiráculos en Thysanoptera tienen una estructura compleja y diversa que indica que funcionan como plastrones que permiten la respiración durante la inmersión por las lluvias o las inundaciones. Se examinaron los espiráculos del mesotórax, metatórax y primer segmento del abdomen de los adultos machos y hembras de 4 especies de Phlaeothripidae que habitan los Desiertos Mojave y Sonora. Los espiráculos tenían poros abiertos rodeados por una red de cutícula. Se observaron 2 clases de estructura de espiráculos, llamados compuesto y simple. La mayoría de los poros en los espiráculos compuestos tiene una mancha de cutícula en el centro. La mayoría de los poros en espiráculos simples no tenian una mancha de cutícula en el centro. Se observaron los espiráculos compuestos en *Leptothrips larreae* Hood. Se observaron los espiráculos simples en *Liothrips xanthocerus* Hood, *Leptothrips fasciculatus* (Crawford), y el trips de ala dimórfica de *Bagnalliella mojave* Hood. Las larvas de primer y segundo instar de *L. larreae* y *L. fasciculatus* tenian la misma clase de espiráculos de los adultos. Los espiráculos del metatórax en las hembras de la forma macróptera de *B. mojave* fueron un poco más grandes que los de las hembras braquípteras. Un adulto vivo del *L. larreae* sumergido en agua, y iluminado oblicuamente desde arriba, reflejó luz desde sus espiráculos del pterotórax, que indica que ellos atrapan el aire y probablemente funcionan como plastrones. Se examinó los espiráculos del pterotórax en especimenes del museo montados en laminas de hembras adultas de 8 especies adicionales de la family Phlaeothripidae registrados en California de localidades en el desierto o en plantas del desierto. Cuatro especies tienen espiráculos compuestos y 4 especies tienen espiráculos simples. Estos 2 tipos de espiráculos son independientes del tamaño del cuerpo. La clase del espiráculo fue ligermente, y no significativa, dependiente de la braquípteria en cualquiera de los sexos. Todas las 4 especies con machos o hembras braquípteros producen hembras adultas con espiráculos simples. De las 8 especies que tienen sólo la forma macróptera, 5 especies tenian espiráculos compuestas, y 3 especies tenian espiráculos simples. Los espiráculos simples pueden ser más comunes en los Phlaeothripidae del desierto que producen formas braquípteras y viven en microhábitats encerrados, que proveen una mayor protección contra la inmersión por precipitación.

Palabras Clave: Insecta, Tubulifera, plastrones, dimorfismo de ala, fotomicrografías

Spiracles, or stigmata, are openings on insect cuticle where tracheae attach. Spiracles may include subcuticular chambers, or atria, and surrounding sclerites called peritremes (Snodgrass 1935). Thysanoptera adults have paired spiracles on the pleura of the mesothorax and metathorax and on the first and eighth abdominal tergites (Moritz 1997). Spiracles on thrips are larger in diameter than their attached tracheae (Fig. 2.18, Moritz 1997), and the spiracular peritremes have a varied and complex structure (Moritz 1985). A scanning electron micrograph (SEM) of a thoracic spiracle (considered here as metathoracic) on an adult female *Gynaikothrips ficorum* (Marchal) (Phlaeothripidae) shows a hemispherical peritreme composed of roughly-textured white and gray cuticle containing numerous, jaggedly-circular, black openings or pores (Fig. 9, Moritz 1985). Each pore contains at its center 1, or sometimes 2, white cuticular spots. Cuticle appears white or gray, and openings in the cuticle black, because the SEM imaged electrons emitted from the spiracle's surface. This intricate structure suggests that spiracles on thrips function as plastrons (Moritz 1985, 1997).

Plastrons are adaptations of the cuticle that repel water, trap air, and allow respiration during submergence (Marx & Messner 2012). They are common and diverse features on terrestrial and aquatic arthropods (Marx & Messner 2012), especially on aquatic insects (Hinton 1968). Plastrons on large, aquatic arthropods are revealed by silvery light reflected by air trapped on the body surface (Pedersen & Colmer 2008). Silvery light reflected by air trapped on and beneath the cuticle has also been observed on submerged thrips (Moritz 1985). Plastrons on terrestrial insects including thrips would enable respiration during temporary periods of rainfall or flooding (Hinton 1968; Moritz 1985). Thysanoptera inhabiting North American deserts may be susceptible to submergence from rainfall, especially during the heavy, localized rains that occur in summer convective storms.

I examined the spiracles on 12 species of Phlaeothripidae recorded in California at desert localities or on desert plants. Four species were examined in greater detail. These were *Liothrips xanthocerus* Hood (1927), *Bagnalliella mojave* Hood (1927), *Leptothrips fasciculatus* (*Phyllothrips fasciculata* Crawford 1909), and *Leptothrips larreae* Hood (1938). *Liothrips xanthocerus* larvae and adults live between young leaves clustered together at the ends of stems on *Pluchea sericea* (Asterales: Asteraceae) (Wiesenborn 2011). This perennial, streamside plant occurs throughout the Mojave and Sonoran Deserts. *Bagnalliella mojave* lives between young leaves clustered together at the center of leaf rosettes on Joshua trees, *Yucca brevifolia* Engelmann (Liliales: Liliaceae) (Cott 1956). Joshua trees are large, perennial monocots indicative of the Mojave Desert. Two wing-morphs occur in *B. mojave*; females are macropterous or brachypterous (or micropterous), and males are brachypterous. *Leptothrips fasciculatus* larvae live inside flowers, and involucres surrounding flower clusters, on *Eriogonum fasciculatum polifolium* (Bentham) (Polygonales: Polygonaceae) (Wiesenborn 2012). Adults are found on and within inflorescences. *Eriogonum f. polifolium* is a small perennial shrub distributed throughout the Mojave and Sonoran Deserts. *Leptothrips larreae* has been collected mostly on creosote bush, *Larrea tridentata* (D.C.) Coville (Sapindales: Zygophyllaceae) (Cott 1956). Creosote bush is ubiquitous throughout the Mojave and Sonoran Deserts.

The following questions were considered: (1) Are the structures of spiracles on adults different among species of desert Phlaeothripidae? (2) Do the structural differences between species also occur in larvae? (3) Do the spiracles repel water and trap air, allowing them to function as plastrons? (4) Are the structures of spiracles on desert phlaeothripids dependent on body size or wing morph?

Materials And Methods

Species of Phlaeothripidae were collected in the Mojave and Sonoran Deserts. *Leptothrips larreae*, *B. mojave*, and *L. fasciculatus* were collected in the Mojave Desert near Nelson (918 m asl) and Searchlight (1085 m asl) in Clark County, southern Nevada. I collected *L. larreae* larvae and adults from *L. tridentata* during April, August, and September 2013. Thrips were swept from plants, rinsed with 10% EtOH from terminal stems supporting leaves, or extracted with a Berlese funnel from green stem-galls caused by the midge, *Asphondylia auripila* Felt (Diptera: Cecidomyiidae) (Russo 2006). I collected *B. mojave* from *Y. brevifolia* during July 2011 and October 2013. Macropterous and brachypterous females between young leaves at the center of leaf clusters were transferred with a moistened brush into 70% EtOH. Collected adults and larvae were treated with NaOH to increase transparency, or untreated, dehydrated in EtOH, and mounted in euparal on slides. I examined adult females with a compound microscope and identified *L.*

larreae with Mound and Kibby (1998) and Cott (1956) and *B. mojave* with Cott (1956). Antennal sense-cones were viewed with phase contrast. I also compared slide-mounted females of both species with specimens in the Ewart Collection at the Entomology Research Museum, University of California, Riverside (UCRC). *Leptothrips fasciculatus* larvae and adults were collected from inflorescences on *E. fasciculatum* during May 2011 and October 2012 (Wiesenborn 2012). *Liothrips xanthocerus* adults were collected from leaf clusters on *P. sericea* alongside the Colorado River in the Sonoran Desert near Topock, Mohave County, and Cibola, La Paz County, Arizona (Wiesenborn 2011). I deposited voucher slides of *L. larreae* larvae and adults (nos. 417193-417197) and both wing-morphs of *B. mojave* (nos. 417188-417192) at UCRC. Slides of larvae and adults of *L. fasciculatus* (nos. 311452-311456) and *L. xanthocerus* (nos. 294624 & 294627-294631) were previously deposited at UCRC.

Spiracles on larvae and male and female adults of *L. larreae* and *L. fasciculatus*, and on male and female adults of *B. mojave* and *L. xanthocerus*, treated with NaOH and mounted on slides were examined. Second-instar larvae were distinguished from first instars by their longer antennal segments as illustrated in Phlaeothripidae by Heming (1991). Sexes of adults were differentiated following Stannard (1968). I examined the mesothoracic spiracles on first instars of *L. larreae* and *L. fasciculatus* at 400X with a compound microscope. I photographed the mesothoracic spiracles on second instars, and the mesothoracic, metathoracic, and first-abdominal spiracles on adult females of both species. A metathoracic spiracle on an adult male *L. larreae*, an adult female *L. xanthocerus*, and on a macropterous and a brachypterous female of *B. mojave* was also photographed. I digitally photographed individual spiracles through a 100X, oil-immersion objective with an achromat condenser and brightfield Köhler-illumination. Photomicrographs at different focal-planes were combined with CombineZP software (Hadley 2013).

Brightfield photomicrographs of spiracles on Phlaeothripidae were interpreted by examining adult female *G. ficorum* from UCRC that had been treated with KOH to increase transparency and mounted on slides. I compared the metathoracic spiracles at 400X in brightfield with Moritz's (1985) SEM of a metathoracic spiracle on *G. ficorum*. The spiracle in brightfield, resembling that on *L. larreae* (Fig. 1d), was a negative image of the SEM. This reversal occurred because brightfield photomicrographs image light transmitted through the specimen, whereas SEM's image electrons emitted from the specimen's surface. Darker areas on the photomicrographs represent greater opacity. The dark areas in the photomicrographs of spiracles on Phlaeothripidae are cuticle, and the roughly-circular, light areas are the pores on the spiracle's surface.

Pterothoracic spiracles on a live *L. larreae* adult female submerged in water were examined and photographed to determine if they trap air. I collected live thrips by heating green stem-galls cut from *L. tridentata* on 29 Sep 2013 in the Berlese funnel. An adult female evacuating a gall was transferred with a moistened brush onto a depression slide containing water and covered with a cover slip. The submerged thrips was illuminated obliquely from above and photographed through the compound microscope. Trapped air was detected by increased reflectance.

Spiracles on other desert species of Phlaeothripidae recorded in California and available in the Ewart Collection at UCRC were examined. Species were selected if the collection data in Cott (1956) included a desert locality or a source plant that typically occurs in the desert. I examined 2 slides of macropterous females of each species treated with KOH. Mesothoracic and metathoracic spiracles were viewed at 400X and classified as compound or simple. All spiracles contained numerous, roughly-circular pores each surrounded by darker cuticle. In compound spiracles, most of the pores contained 1, or sometimes 2, dark spots of cuticle at their center as seen on *L. larreae* (Fig. 1d). In simple spiracles, most of the pores lacked these spots as seen on *L. fasciculatus* (Fig. 1h).

Dependence of spiracle structure on body length, and interaction between spiracle structure and wing morph, among species was tested. Body lengths of macropterous females, and wing morphs of females and males, were obtained from Cott (1956). I compared body lengths between species with simple or compound spiracles with a *t*-test (Systat version 10.2, Chicago, Illinois). Species were classified as only macropterous or as brachypterous in either sex. I tested for interaction between the 2 classes of wing morph and the 2 classes of spiracle structure with a 2-tailed Fisher's exact test. Fisher's exact tests are used for small sample sizes and calculate the probability of the observed frequencies plus the probabilities of more-lopsided frequencies favoring non-independence.

RESULTS

Three pairs of spiracles were observed on or near the pterothorax of female *L. larreae* (Fig. 1a) and *L. fasciculatus*. One pair is on the anterior corners of the mesothorax. On *L. larreae*, these spiracles are elliptic and curve posteriad onto the side of the thorax (Fig. 1c). The mesothoracic spiracles on *L. fasciculatus* are smaller and ovoid and reside entirely on the dorsum (Fig. 1g). The second pair of spiracles occurs on the anterior margin of the metapleuron near the metanotum. These metapleural spiracles are similar in *L. larreae* (Fig.

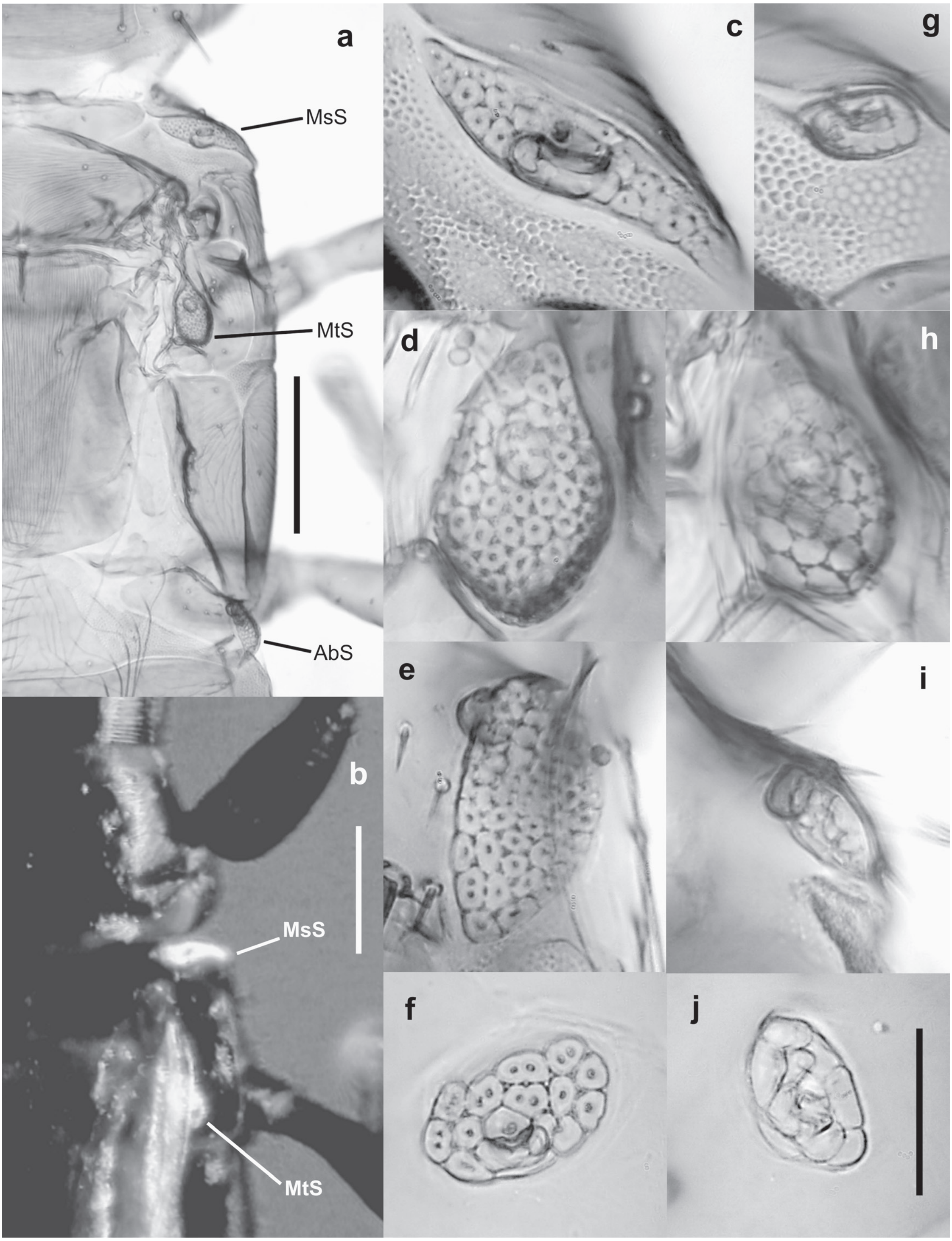

Fig. 1. a. Right-dorsal pterothorax of NaOH-treated, adult female *Leptothrips larreae*,vertical bar is 100 µm: MsS, mesothoracic spiracle; MtS, metathoracic spiracle; AbS, first-abdominal spiracle. b. Right dorsum of live, adult *L. larreae* submerged in water and illuminated obliquely from above, vertical bar is 100 µm: MsS and MtS (partially beneath wings) as above. c–e. Adult female *L. larreae*: c, right mesothoracic spiracle; d, right metathoracic spiracle; e, right first-abdominal spiracle. f. Second instar *L. larreae*, left mesothoracic spiracle. g–i. Adult female *Leptothrips fasciculatus*, same spiracles as c–e. j. Second instar *L. fasciculatus*, left mesothoracic spiracle, vertical bar is 25 µm. Photomicrographs c–j are at same scale.

1d) and *L. fasciculatus* (Fig. 1h), lie alongside the base of the hind wings, face entirely dorsad, and are ovate. The third pair of spiracles lies on lateral lobes of the first abdominal segment. The first-abdominal spiracles are dorsolateral on *L. larreae* and ventrolateral on *L. fasculatum*. The right spiracle on *L. fasculatum* (Fig. 1i) was photographed through the setae-bearing, abdominal lobe. The first-abdominal spiracles on *L. larreae* are half-circular and extend to the segment's margin (Fig. 1e). On *L. fasciculatus*, they also extend to the segment's margin but are smaller.

Spiracles differ between *L. larreae* and *L. fasciculatus* adults. Pores on mesothoracic, metathoracic, and first-abdominal spiracles contain central spots of cuticle in females of *L. larreae* but not *L. fasciculatus*. Most pores on *L. larreae* contain 1 spot, although some pores may be without spots (Fig. 1d, upper left) or contain 2 of them (Fig. 1e, lower left). The pores on metathoracic spiracles are larger in *L. fasciculatus* (Fig. 1h) than in *L. larreae* (Fig. 1d). Spiracles on male *L. larreae*, such as the metathoracic (Fig. 2a), resemble those on females but have fewer pores containing cuticular spots. Spiracles on *L. fasciculatus* males contain pores without cuticular spots, similar to those on females. A blurred oval was evident on photographed spiracles, especially near the center of metathoracic spiracles (Figs. 1d,h & 2a,d). The oval came into focus slightly below the peritreme's surface. A similar oval was seen with brightfield microscopy on the metathoracic spiracles of *G. ficorum* and is the depressed region near the spiracle's center shown in the SEM (Moritz 1985).

The compound spiracles on adult *L. larreae*, and the simple spiracles on adult *L. fasciculatus*, also occur on larvae. The mesothoracic spiracles on both larval instars of *L. larreae* are compound, and many of the pores on second instars contain 2 cuticular spots (Fig. 1f). These spots are absent in the pores on the mesothoracic spiracles in first instar and second instar (Fig. 1j) *L. fasciculatus*.

Macropterous and brachypterous *B. mojave* females support slightly different metathoracic spiracles. Spiracles are larger, more rounded, and with more-distinct pores in macropters (Fig. 2b) compared with brachypters (Fig. 2c). Metathoracic spiracles in males, all brachypterous, resemble those in brachypterous females. Spiracles in both wing morphs and sexes of *B. mojave* are simple. Spiracles of male and female *L. xanthocerus* are also simple, although faint spots of cuticle are evident in some pores on the metathoracic spiracles of females (Fig. 2d). Mushroom-shaped projections of cuticle, continuous with the dark cuticle surrounding the peritreme's pores, are visible at the lateral edge of the left metathoracic spiracle on *L. xanthocerus* (Fig. 2e).

Light from trapped air was reflected by the mesothoracic and metathoracic spiracles on the live, adult *L. larreae* submerged in water (Fig. 1b). Nearly the entire surface-area of both spiracles produced a strong reflection that contrasted with the surrounding exoskeleton. When viewed at higher magnification (Fig. 2f), the reflection was comprised of dots that corresponded with the spiracular pores (Fig. 1c). An area of non-reflectance appeared on each pterothoracic spiracle (Fig. 1b) that exhibited a circular shape on the mesothoracic spiracle at higher magnification (Fig. 2f). These areas of non-reflectance roughly matched the blurred ovals on the same spiracles of *L. larreae* (Fig. 1c,d). The forewings and hindwings partially overlaying the metathoracic spiracles also reflected light (Fig. 1b). This reflectance was less intense and more uneven than reflectance from the spiracles.

Simple spiracles were more common than compound spiracles on adult females of desert Phlaeothripidae. Simple spiracles were found on 7 species in 5 genera and 2 tribes, and compound spiracles were found on 5 species in 3 genera and 2 tribes (Table 1). All species of *Leptothrips* supported compound spiracles except for *L. fasciculatus*. *Liothrips* contained 1 species with simple spiracles and 1 species with compound spiracles. All 3 species of *Bagnalliella* had simple spiracles, although cuticular spots were seen in some pores on the mesothoracic spiracles of *Bagnalliella desertae* Hood and *Bagnalliella yuccae* (Hinds). Body lengths of adult females did not differ (t = 0.36, df = 10, P = 0.73) between species with compound (mean 2.0, 1.8-2.3 mm) or simple (2.0, 1.0-2.3 mm) spiracles.

Spiracle structure weakly, and non-significantly, interacted with brachyptery in either sex (P = 0.081). Eight species produced only macropters, 3 species produced macropterous and brachypterous females and brachypterous males, and 1 species produced macropterous females and brachypterous males (Table 1). Four species therefore were classified as brachypterous in either sex. All species with brachypterous males or females produced adult females with simple spiracles. Of those with only macropters, 5 species supported compound spiracles, and 3 species supported simple spiracles. Macropterous species with simple spiracles were *Haplothrips malifloris* Hood, *L. fasciculatus*, and *L. xanthocerus*.

DISCUSSION

The structure of the spiracles on desert Phlaeothripidae can be inferred from the photomicrographs and from the SEM of the metathoracic spiracle on *G. ficorum* (Moritz 1985). Spiracular peritremes appear to be composed of irregularly-shaped projections of cuticle that are visible on *L. xanthocerus* and, in reverse brightness, at the upper edge of the spiracle on *G. ficorum* (Moritz 1985). These projections narrowly interconnect

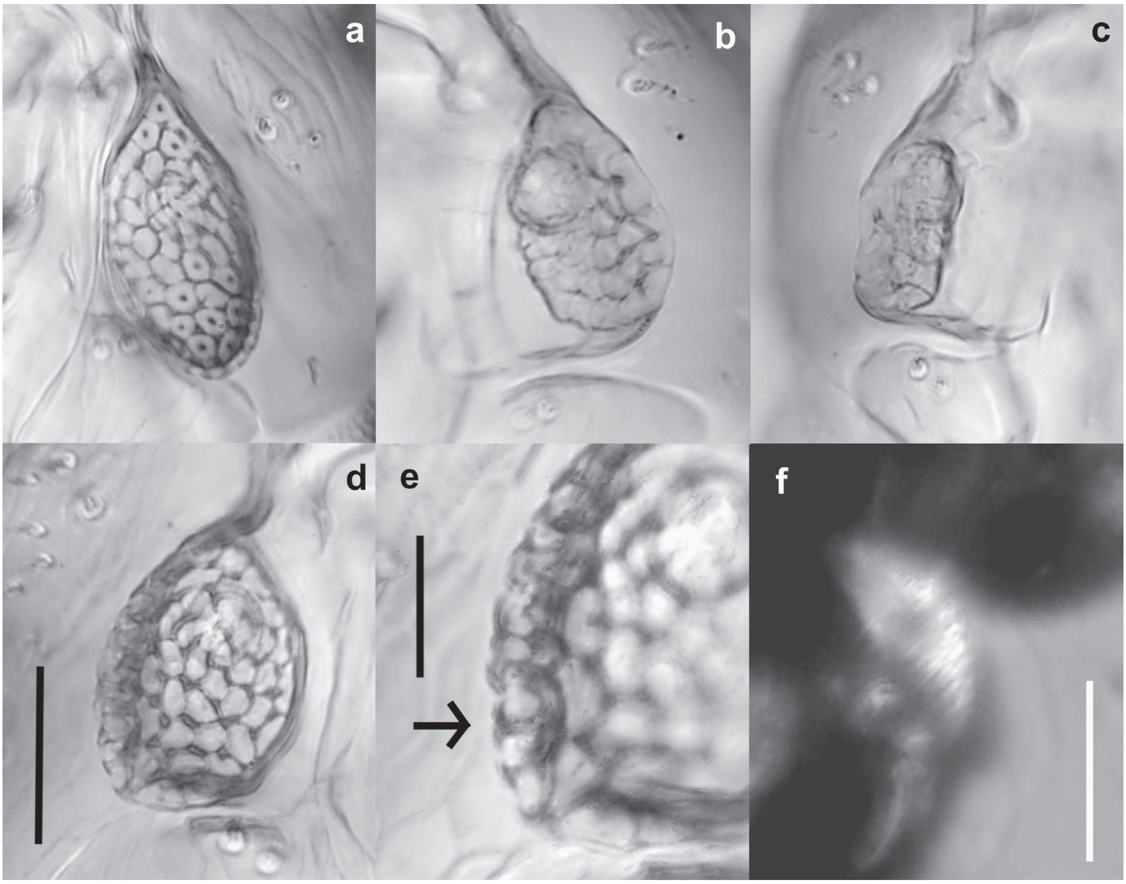

Fig. 2. a–e. Metathoracic spiracles: a, adult male *Leptothrips larreae*, right spiracle; b, macropterous female *Bagnalliella mojave*, right spiracle; c, brachypterous female *B. mojave*, left spiracle; d, adult female *Liothrips xanthocerus*, left spiracle, vertical bar is 25 µm; e, close-up of left spiracle on *L. xanthocerus*, vertical bar is 10 µm, arrow points to cuticular projection in side view. f. Close-up of reflectance from right mesothoracic spiracle on live, adult *L. larreae* submerged in water and illuminated obliquely from above, vertical bar is 50 µm. Photomicrographs a–d are at same scale.

to form a primary network of fused cuticle. Circular openings with angular margins within the network act as pores. Pores on compound spiracles also contain an additional projection (or 2 projections) of isolated cuticle at their center. Hinton (1968) described the plastrons found in spiracular gills of aquatic pupae. The plastrons are formed by upward projections of the cuticle, termed columns or struts, which flatten and fuse at the surface. Struts may be unbranched or branch dendritically, as in black flies (Diptera: Simuliidae), or branch apically as in a marine crane fly (Diptera: Tipulidae) (Figs. 43 and 48, Hinton 1968). Spiracles on desert phlaeothripids appear to have similar construction, except that compound spiracles also contain struts that remain separate.

Development of simple or compound spiracles within species appears consistent between sexes and across life stages. Similar spiracles in both larval instars and adult females suggest that all 3 life stages within species are exposed to similar environmental conditions. The spiracles on quiescent life-stages, instars more difficult to collect, remain to be examined.

The slightly larger and more-rounded metathoracic spiracles in macropterous *B. mojave* females, compared with brachypters, suggests that spiracle structure is associated with the respiratory requirements of flight. Macropterous thrips would be expected to have larger pterothoracic spiracles than brachypterous or apterous thrips. Different spiracles between wing morphs also suggest that brachypterous *B. mojave* females are not dealated macropters. Truncated wing loss by macropterous females in Phlaeothripidae has been observed in a species that feeds on fungus in England (Moritz 2002) and several species that inhabit leaf domiciles in Australia (Mound & Morris 2001).

TABLE 1. SPIRACLE STRUCTURE AND BODY LENGTH OF MACROPTEROUS FEMALES, AND WING MORPHS OF FEMALES AND MALES, OF PHLAEOTHRIPIDAE RECORDED IN CALIFORNIA DESERTS.

Tribe	Genus	Species	Spiracle structure[5]	Body length (mm)	Wing morphs females[6]	Wing morphs males[6]
Hoplothripini	*Liothrips*	*lepidus*[2]	compound	1.9	M	M
		xanthocerus	simple	2.3	M	M
	Scopaeothrips[1]	*bicolor*[3]	simple	1.0	M & B	B
Haplothripini	*Bagnalliella*	*desertae*	simple	2.3	M & B	B
		mojave	simple	2.1	M & B	B
		yuccae[2]	simple	1.6	M	B
	Haplothrips	*malifloris*[2]	simple	2.2	M	M
	Karnyothrips	*flavipes*[2]	compound	2.3	M	U
	Leptothrips	*distalis*[2,4]	compound	2.0	M	M
		fasciculatus[2,4]	simple	2.2	M	M
		larreae	compound	2.2	M	M
		purpuratus[4]	compound	1.8	M	M

Species in Ewart Collection, Entomology Research Museum, University of California, Riverside; geographic distributions, body lengths, and wing morphs from Cott (1956).

[1] *Rhopalothrips* in Cott (1956).

[2] Not restricted to desert.

[3] Included due to specialization on *Opuntia* (Caryophyllales: Cactaceae) (Cott 1956).

[4] *Haplothrips* in Cott (1956).

[5] Mesothoracic and metathoracic spiracles; most pores in compound spiracles contain cuticular spots, most pores in simple spiracles lack cuticular spots.

[6] B, brachypterous (or micropterous); M, macropterous; U, males unknown.

Spiracles on desert Phlaeothripidae appear to function as plastrons by repelling water and trapping air. Reflectance by the pterothoracic spiracles on *L. larreae* agrees with Moritz's (1985) observation of trapped air on submerged thrips. Similarity between the pattern of reflectance and the pattern of pores on *L. larreae*'s mesothoracic spiracle suggests that water contacts the cuticular network, and air is retained beneath the pores in the atrium. Moritz (1995) also described the exclusion of water from the spiracular atrium, or vestibule. Air is apparently not trapped in the smaller, circular area on the spiracle where light was not reflected. This region of non-reflectance, roughly corresponding with the peritreme's sunken surface, may be associated with a dense, central cluster of supporting struts or the attachment of the underlying trachea.

Thysanoptera may not require the large plastrons, relative to body size, observed on larger aquatic insects with tracheae (Pedersen & Colmer 2008). Exchange of oxygen between water and trapped air is limited by the area of contact between the two media (Hinton 1968). In contrast, the metabolic demand of insects is related to body volume. Plastron size, a square function, and respiratory requirement, a cube function, interact subject to scaling. Plastrons covering a small proportion of the body surface of thrips, such as the spiracles on *L. larreae*, may provide a temporarily-adequate area of gas exchange relative to body volume. Thrips submerged by rainfall would likely also be inactive and respire less. Other structures, such as the wings, may supplement the spiracles with trapped air.

Susceptibility to submergence may vary among species of desert Phlaeothripidae. Species that spend part of their life cycle in soil or litter would be especially vulnerable to submergence following rainfall. For example, *L. fasciculatus* inhabits soil and litter beneath plants as late second-instar larvae, propupae, pupae, and newly-developed adults when flowers on its host plant are unavailable (Wiesenborn 2012). Plastrons on these life stages would increase survival by enabling respiration within saturated soil. Propupae and pupae of *L. xanthocerus* likely also overwinter in soil and leaf litter beneath plants (Wiesenborn 2011). Plastrons may also provide an advantage to life stages of Phlaeothripidae that do not inhabit soil or litter. *Bagnalliella mojave* appears to complete its life cycle entirely between the leaves on *Y. brevifolia*, because both larval instars and a propupa were collected alongside the adults during October. The presence of plastron-like spiracles on *L. larreae* and *L. fasciculatus* first-instar larvae, a life stage of plant-inhabiting thrips typically not found in soil or litter, also suggests these species risk submergence on plants.

Compound spiracles provide a denser network of cuticle than simple spiracles. This is best seen by comparing the metathoracic spiracles of *L. larreae* and *L. fasciculatus*. Pores on *L. larreae*'s spiracles are smaller and with central spots of cuticle. This arrangement provides a greater surface area of cuticle for resisting water, but would likely impede respiratory air flow more than the surface of simple spiracles. Larger spiracles, as seen on the mesothorax and first-abdominal segment of *L. larreae* compared with *L. fasciculatus*, may compensate for increased air-flow resistance. Larger species did not produce the more-complicated compound spiracles, as simple spiracles were found on 2 of the 3 largest phlaeothripids (*L. xanthocerus* and *B. mojave*).

Weak dependence between spiracular structure and wing morph may be due to both body features being associated with microhabitat. Many of the species producing brachypters, which all had simple spiracles, live in confined microhabitats. For example, the 3 species of *Bagnalliella* live between young leaves that are tightly clustered together at the center of leaf rosettes on *Yucca* (Cott 1956). Two of the 3 species that were entirely macropterous, but with simple spiracles, also live in confined microhabitats. *Liothrips xanthocerus* larvae and adults live between leaves that are pressed tightly together in leaf clusters (Wiesenborn 2011). *Leptothrips fasciculatus* larvae live inside tubular, 3 mm-long flowers and 3-4 mm-deep involucres that surround flower clusters (Wiesenborn 2012). The other *Liothrips* examined, *L. lepidus*, has compound spiracles and appears to inhabitat more-open spaces. *Liothrips lepidus* adults have been collected by beating oak trees, *Quercus* sp. (Fagales: Fagaceae) (Cott 1956). The microhabitat used by larvae and adults of the other *Leptothrips* is unknown. Most members of the genus are believed to be predators (Cott 1956; Mound & Minaei 2007), an exception being *L. fasciculatus* (Wiesenborn 2012). *Leptothrips larreae* appears to use various microhabitats, because larvae and adults were collected from stem galls and from stems without galls. Mortality from submergence in rainfall may be less likely in the nearly-enclosed spaces inhabited by species with simple spiracles. Development of simple or compound spiracles in desert Phlaeothripidae may be an evolutionary balance between maximizing respiration efficiency and minimizing mortality from submergence due to rains.

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