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A new species of *Lachesilla* Westwood (Psocoptera: Lachesillidae) in the *andra* group with a proposed classification of the *andra* group

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Abstract

We describe *Lachesilla texana* Mockford and García Aldrete, **n. sp.**, with populations in northeastern Mexico, central and southern Texas, and Great Smoky Mountains National Park, Tennessee. Several minor differences are noted between the Smoky Mountains and the Texas-Mexican populations. We assign the new species to the *andra* group (García Aldrete 1974) and in order to place it within this large and complex species group, we propose a classification of the group with designation of four subgroups based primarily on male external genitalic and paragenitalic structures. Probable apomorphies are noted for each of the subgroups.

Keywords: Psocoptera, Lachesillidae, *Lachesilla*, Mexico, Texas, Tennessee, new species, disjunct distribution

Introduction

Psocoptera from the biological survey of the Great Smoky Mountains National Park (Parker and Bernard, 2006) were sent to ELM for identification. The material included an undescribed species in the large genus *Lachesilla*. Its affinities in the genus became clear only with the recent find of a single male. It has proven to be the same as an undescribed species long known to the authors from central and southern Texas and northern Mexico. The sample from the Smoky Mountains consists currently of only two females and one male. Comparison of this tiny sample with the much larger Texas-Mexican sample reveals several minor differences; however, the similarities are so overwhelming that we have chosen to call all a single species. If, later, more material becomes available from the Smoky Mountains or intervening localities, it may be necessary to revise this opinion.

The new species is assigned to the *andra* group (García Aldrete, 1974), and to clarify the relationships of species within this group, we propose a group classification based primarily on the great diversity of male terminal abdominal structures, supplemented with other structural and color characters of both sexes.

Material and Methods

The description of the new species is based on examination of the Smoky Mountains material plus ten males and 18 females of the Texas-Mexican material. Illustrations were made with the aid of a drawing tube (body parts) and microprojector (wings). Measurements (in microns) were made on slide-mounted parts (except IO/d measurements on whole, unmounted heads) with a filar micrometer. Color descriptions are based on observations through a dissecting microscope with direct light on specimens preserved in 80–95% ethyl alcohol for various periods of time. Photographs were taken with a ProgRes™C10 camera on a dissecting microscope (whole specimen) and on a compound microscope (body parts).

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Abbreviations used for measurements, etc. are as follows: F = hind femur; f1–f4 = first to fourth flagellomeres; FW = forewing; HW = hindwing; IO/d = least distance between compound eyes divided by lateral diameter of a compound eye in either dorsal or anterior view; P4 = distal segment of maxillary palpus; T = hind tibia; t1 and t2 = hind first and second tarsomeres; t1ct = number of ctenidia (comb-based setae) on hind first tarsomere.

The holotype and topotypic paratypes will be deposited in the Institute of Biology, Universidad Nacional Autónoma de México, Mexico City (IBUNAM). Most of the other Texas and Mexican paratypes will be placed in that collection, while others, including the Smoky Mountains specimens, will be placed in the Illinois Natural History Survey, Champaign, Illinois (INHS).

***Lachesilla texana* sp. n.**

Diagnosis. Habitus (Fig. 1). Species of the *andra* group (*sensu* García Aldrete, 1974), sharing with *Lachesilla mayorgae* García Aldrete (2000) absence of hypandrial claspers (possibly represented in this species by a pair of rugose turrets on the hypandrium), dark P4, and radial spots in cells R5 and M1–M3 of the forewing. Differing from *L. mayorgae* in absence of distal seta on each terminal hypandrial lobe, presence of a medially-directed serrulate-tipped blade arising on inner surface of each distal hypandrial lobe, and presence of a subapical turret on each distal hypandrial lobe.

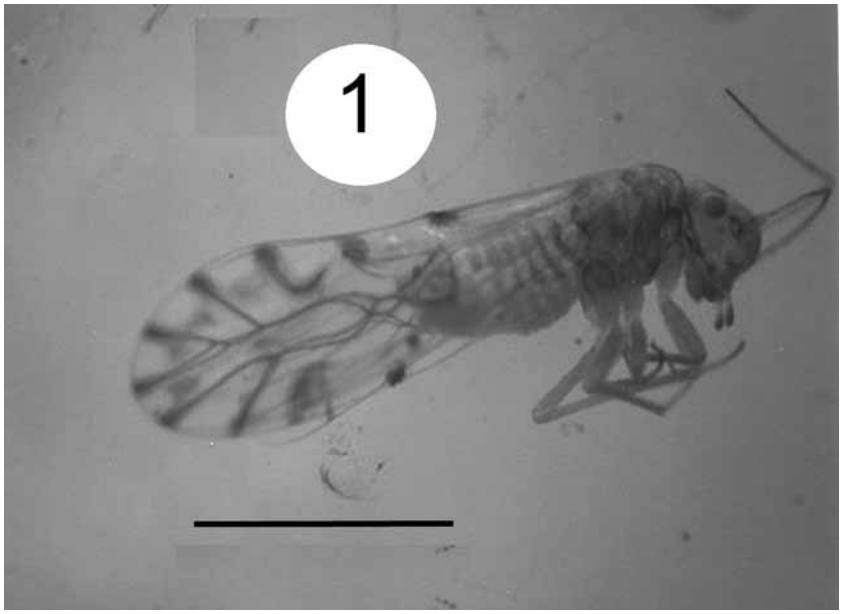
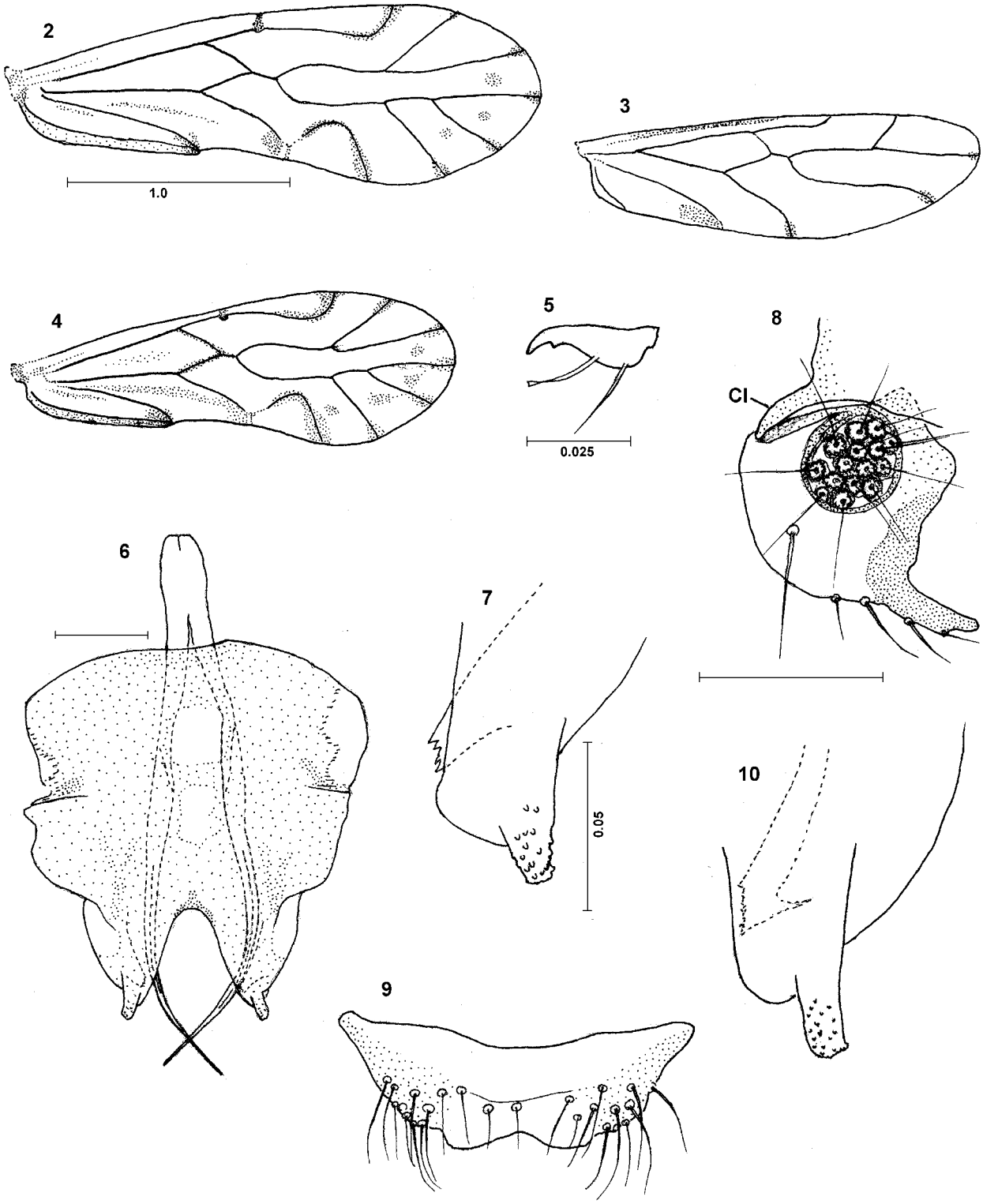
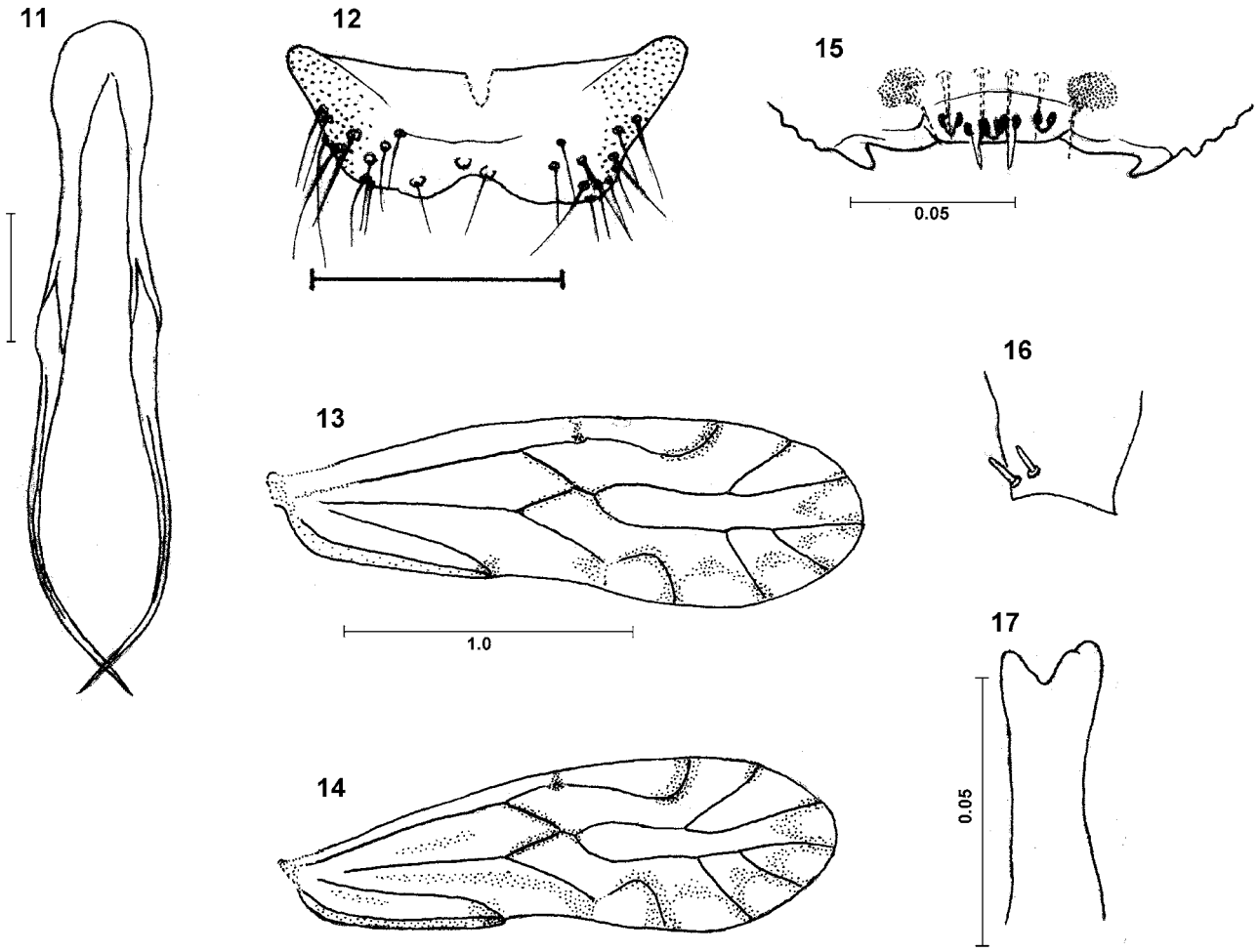


FIGURE 1. *Lachesilla texana* **n. sp.** Female, lateral view, freshly preserved specimen (San Marcos, T**exas).** Scale bar = 1.00 mm.

Male color (specimen from northern Mexico, in alcohol 33 years). Compound eyes black; remainder of head creamy white with straw-brown areas as follows: band bordering median ecdysial line, spot bordering each eye dorso-medially, 8 relatively broad bands running lengthwise through postclypeus and converging antero-ventrally. Ocelli colorless; frons with a median brown spot darker than surroundings. Antennae medium brown; P4 dusky purplish-brown; remainder of mx palpus straw brown. Thorax creamy yellow except straw brown on notal lobes; suture lines reddish-brown. Legs straw brown, the tarsi somewhat darker brown. Forewing membrane very pale brown-washed; forewing marked as in Fig. 2; dark brown radial spots in cells R5, M1, M2, and M3; dark brown spots at distal ends of R, M, and Cu veins. Hindwing (Fig. 3) with a cloudy brown spot at marginal end of each vein; spot at end of Cu2 only on basal side of vein. Preclunial abdominal segments each with a slender reddish-brown transverse band of subcuticular pigment, absent ventrally, on creamy yellow background. Clunium creamy yellow but brown along anterior margin and at paraproctal articular areas. Hypandrium and paraprocts brown; epiproct creamy yellow.



FIGURES 2–10 *Lachesilla texana* **n. sp.**, male. (2) Forewing (type, north Mexico); (3) Hindwing (type); (4) Forewing (Great Smoky Mountains); (5) Pretarsal claw (type); (6) Hypandrium and phallosome (type); (7) Distal lobe of hypandrium (north Mexican paratype); (8) Paraproct and clunial articular region, Cl=clunial arm (type); (9) Epiproct (type); (10) Distal lobe of hypandrium, enlarged (Great Smoky Mountains). Scale bars = 0.1 mm unless indicated otherwise. Figs. 2, 3, and 4 to common scale; Fig. 9 to scale of Fig. 8; Fig. 10 to scale of Fig. 7.



FIGURES 11–17. *Lachesilla texana* **n. sp.** (11) Male, phallosome (Great Smoky Mountains); (12) Male, epiproct (Great Smoky Mountains); (13) Female, forewing (north Mexican paratype); (14) Female, forewing (Great Smoky Mountains); (15) Female, free margin of labrum (north Mexican paratype); (16) Female, paired basal sensilla of P4 (north Mexican paratype); (17) Female, lacinial tip (north Mexican paratype). Scale bars = 0.1 mm unless indicated otherwise. Fig. 14 to scale of Fig. 13. Fig. 16 to scale of Fig. 17.

Male color differences of Great Smoky Mountains specimen (in alcohol 2 years). Most of head pale brown but white on parietal region of vertex and posterior and ventral edges of genae; the brown areas indicated above slightly darker; lateral ocelli brown, the median colorless; longitudinal bands of postclypeus reddish-brown. Antennal scape, pedicel, and f1 creamy white, remainder of flagellum brown. Legs creamy yellow except tarsi pale brown. Forewing (Fig. 4) as described above but with a pale longitudinal brown band in basal R cell and a darker brown band running the length of cell Cu1b.

Male structural characteristics: head and thorax. Median ecdysial line distinct to ocellar field; frontal lines not visible. Lateral ocelli large and round, somewhat separated from smaller, lenticular median ocellus. Compound eyes small, IO/d range for 4 specimens = 3.16– 3.53 . Antennae ca. equal to body length. Free margin of labrum, basal sensilla of P4, and lacinial tip as described for female. Forewing (Fig. 2) relatively slender, L/W = 2.86; pterostigma rounded posteriorly, relatively deep; Rs-M junction a long fusion, almost half length of first Rs segment; Rs curved (arched) forward distal to Rs-M junction, the Rs fork stem ca. equal in length to vein R4+5 ; areola postica relatively large. In hindwing, Rs-M junction a long fusion. An inner row of setae on hind tibia with black basal scales, the row becoming double in distal half of tibia; a few setae in outer row of hind tibia also with black basal scales; middle tibia with 6–7 setae in inner row with black basal scales; middle and hind tibiae each with 4 terminal spurs, fore tibia with 3 terminal spurs; each pretarsal claw with a minute preapical denticle, a slender pulvillus slightly widened at its distal end, and a basal seta (Fig. 5).

Differences of Great Smoky Mountains specimen. Compound eyes slightly larger, IO/d = 2.70. Antennae slightly shorter than body length.

Male terminal abdominal characters. Hypandrium (Fig. 6) 2-segmented; distal segment terminating in 2 rounded lobes separated by a deep concavity, each lobe bearing a subdistal rugose turret laterally and a serrate-edged blade arising on its inner surface and projecting medially (enlarged area, Fig. 7). Phallosome (Fig. 6) Consisting of 2 slender apodemes fused basally, ca. 1 1/3x length of hypandrium, each apodeme showing 2 diverging creases at its basal one-third and a groove running from about its middle nearly to its tip. Clunium slightly protruding in middle under base of epiproct; laterally with a horn-shaped process extending to lateral articular point of paraproct (Fig. 8). Paraproct with distal process slender, bluntly pointed or truncated at tip; sensorium basal, compact, with 11–15 trichobothria with basal florets. Epiproct (Fig. 9) transverse, bilobed distally, with broad distal shelf.

Differences of Great Smoky Mountains specimen. Serrate-edged blade of lateral lobe of hypandrium broader at tip (Fig. 10). Base of phallosome (fused area of apodemes) broader (Fig. 11). Clunium slightly excavated in middle before base of epiproct. Distal shelf of epiproct slenderer (Fig. 12).

Male measurements (microns, figure for a male from type locality followed by figure for male from Great Smoky Mountains National Park in parentheses). FW= 2356 (1959); HW= 1762 (1433); F= 369 (315); T= 751 (620); t1= 198 (148); t2= 88 (95); t1ct= 11 (8); f1= 248 (190); f2= 235 (173); f3= 206 (161); f4= 169 (129).

Female color (in alcohol 2 mo.; those in alcohol 33 years as described for the male). Compound eyes pale greenish-gray. Rest of head: vertex white with broad grayish-brown band bordering ecdysial line from hind margin almost to ocellar field; another band of grayish-brown bordering each compound eye mesally; ocelli red-rimmed; a dusky grayish-brown spot on frons in front of ocellar field; postclypeus white with grayish-brown chevron lines; antennal sockets bordered in reddish brown; genae mottled pale gray and white; mouthparts grayish-brown, except P4 dark purplish brown. Antennae grayish-brown from base through f3, dark brown from f4 to tip. Thorax mostly rusty brown, darkest on notal lobes and pale gray between notal lobes. Legs pale grayish brown. Forewing (Fig. 13) hyaline with dark brown spot at marginal end of each vein R1 through nodulus; a distinct subdistal brown spot in cell R5; less distinct brown spot in each of the M cells. Hindwing hyaline with a brown spot bordering marginal end of each vein R2+3 through Cu2 and a vague brown spot in distal end of cell Cu2. Abdomen white with brown rings, incomplete ventrally, in segments 2–7, the rings darkest and somewhat reddish in segments 2 and 3.

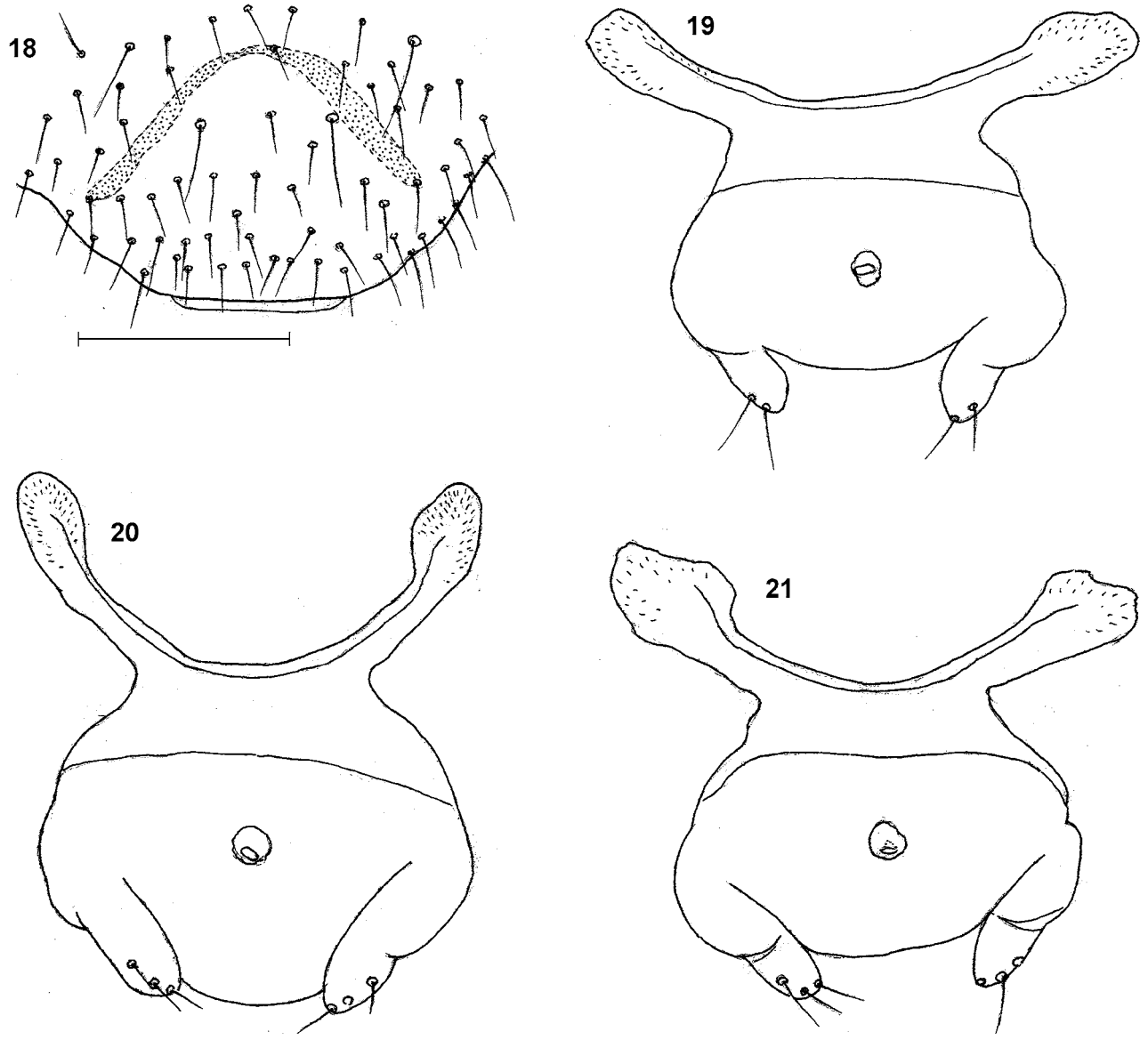
Differences of Great Smoky Mountains specimens (in alcohol 7 years). Border of antennal socket brown, incomplete posteriorly. Median ecdysial line brown bordered only in its posterior half. Thorax in general somewhat paler. Legs straw brown, the tarsi somewhat darker brown than rest of leg. Forewing membrane very pale brown-washed. Forewing markings (Fig. 14) as noted for male.

Female structural characters: head and thorax. Ecdysial lines as described for male. Lateral ocelli smaller than in male, but larger than median ocellus. Compound eyes relatively smaller than in male, IO/d = 3.98. Antennae slightly shorter than body length; sparse, distally slanting setae on all flagellomeres, in length ca. 1.5x width of their segment. Free margin of labrum with short stylets (Fig. 15); inner row of sensilla consisting of two short setiforms alternating with 3 placoids. Paired basal sensilla of P4 (Fig. 16) minute and situated close to base of palpomere. Lacinial tip (Fig. 17) with its 2 tines about equal in length, the lateral broader. Forewing (Fig. 11) proportions much as in male, L/W = 3.12; venation as described for male, but Rs-M junction shorter and areola postica not as high. In hindwing, Rs and M joined a short distance. Legs as described for male except inner row of setae of middle tibia lacking basal scales.

Differences in Great Smoky Mountains specimens. In forewing (Fig. 14), Rs-M junction slightly shorter. In hindwing, a slight cuticular thickening along hind margin of subapical pigment spot of vein Cu2.

Female terminal abdominal characters. Subgenital plate (Fig. 18) with posterior margin straight; a belt of sclerotic thickening curving anteriorly across the plate near hind margin; scattered setae over plate surface, those at and near distal margin, plus 4 others longer. Ovipositor valvulae (Figs. 19, 20) attached basally to 9th sternum, divided into basal and distal regions by a transverse sclerotized band; distal region bearing 3 setae at and near apex. Ninth sternum (Figs. 19, 20) in 2 segments, the distal segment trapezoidal with spermapore in

middle; the proximal segment bearing paired arms with rugose surfaces, broadened at tips. Some Mexican females with the arms curving forward (Fig. 20). Spermatheca folded under distal segment of 9th sternum, with tube broadened immediately after curving back upon itself, ending in a thin-walled sperm sac. Epiproct and paraprocts normal for the genus; paraproctal sensorium with 9–11 trichobothria with basal florets and a peripheral with simple base.



FIGURES 18–21. *Lachesilla texana* **n. sp.** Female. (18) Subgenital plate (north Mexican); (19) Ninth sternum and ovipositor valvulae (Texan); (20) Ninth sternum and ovipositor valvulae (north Mexican); (21) Ninth sternum and ovipositor valvulae (Great Smoky Mountains). Scale bar = 0.1 mm. All figures to same scale.

Differences of Great Smoky Mountains specimens. Subgenital plate with posterior margin slightly depressed in middle. Anterior arms of ninth sternum (Fig. 21) wider distally.

Female measurements (microns, figure for a female from type locality followed by figure for a female from Great Smoky Mountains National Park in parentheses). FW= 2125 (1841); HW= 1578 (1389); F= 347 (316); T= 663 (632); t1= 166 (166); t2= 88 (94); t1ct= 7 (9); f1= 196 (172); f2= 186 (147); f3= 156 (135); f4= 123 (112).

Material studied (collected by ANGA unless indicated otherwise). Holotype, male, MEXICO : Nuevo León: San Nicolás de los Garza, el. 500m, 24 December 1975, in dry Buffel grass; same data, 4♂, 8♀ paratypes (IBUNAM). Additional paratypes: MEXICO: Coahuila: 3km NE Zaragoza, 28 December 1968, 2♀; Nuevo León: Cerro de la Silla, E slope, 7 April 1974, 1♀; same loc., 7 June 1974, on dead grasses, 2♀; same loc, 30 March 1988, 1♂; Cerro de la Silla NW slope, el. 600m, 30 December 2007, 1♂; Cerro de la Silla, W slope, 23 December 1973, beating dried grasses, 3♂, 2♀; El Cerrito nr. Santiago, 30 July 1985, 1♀; 16.1km NE Iturbide, 13 June 1962, beating cycad, *Dioon edule*, 1♂, 1♀, coll. E. L. Mockford & F. Hill. USA: Tennessee: Blount Co.: Great Smoky Mountains National Park: ATBI Plot: Cades Cove, 18 June – 2 July 2001, Malaise trap 03, coll. Stocks & Hightower, 2♀; same loc., 29 August – 14 September 2006, 2-meter Malaise trap, 1♂, coll. J. Gulbransen; Texas: Bell Co.: 2km NE Salado, 2 September 1971, 1♂, 2♀; Hays Co.: Aquarena Springs, 26 February 2009, beating vine, coll. D. Young, 1♀; same loc., 2 March 2009, beating *Myrica cerifera*, coll. D. Young, 1♀; Hill Co.: Lake Whitney State Park, 11 September 1986, 1♂, 1♀; Kerr Co.: Kerrville, 3 April 1958, coll. E. Becker & H. Howden, 1♂, 1♀.

Discussion

The genus *Lachesilla* is one of the larger genera of the order Psocoptera, with some 280 described species, and many awaiting description. García Aldrete (1974) proposed a series of species groups for this genus, which remains the only published attempt at a classification of the entire genus. With increasing knowledge over the years, some of the species groups have been joined with others, while some have expanded, with modifications of criteria for inclusion. Meanwhile, Li Fasheng (1995, 2002) has erected five new genera, primarily for Chinese species, in the subfamily Lachesillinae (*sensu* Mockford and Sullivan, 1986). Some obvious similarities across generic lines have posed difficulties with the application of these genera, and Lienhard (2003) synonymized the genus *Dicrolachesillus* Li (2002) with *Lachesilla*. Critical evaluation of the other genera is still needed.

The *andra* group was one of the groups originally proposed by García Aldrete (1974). Males were known for very few of the originally included species, and the concept of the group was based largely on the very consistent female external genitalia. As more males became known, it also became evident that they represented a great diversity of external genitalic types, and that no characters among them could define this group. To try to resolve this problem, we have searched for additional characters. We find that the mode of articulation of the male paraprocts and clunium is unique within several of the species groups of *Lachesilla*. In most members of the *andra* group it is particularly striking. A long arm from the posterior margin of the clunium (Fig. 8 , see also García Aldrete 2000, Fig. 5 and Li Fasheng 2002, Fig. 1516C) protrudes posteriorly and articulates with a sclerotized ridge along the base of the paraproctal sensorium. This relationship has been consistent for all but two members (see below) of the *andra* group that we have examined. It undoubtedly constitutes a synapomorphy within the group. We have not found it elsewhere in *Lachesilla*. We have examined representatives of all of the (15) other species groups (*sensu* García Aldrete, l974 et seq.) of *Lachesilla* in which males are known. In all but three, the paraproct either joins the clunium directly, or articulates by a short lateral projection of the clunium. In three groups (*magnifica*, *sclera*, and *palmicola*), the lateral projection of the clunium is somewhat longer, but in no case is it as long and as posteriorly-directed as in the *andra* group.

Female genitalic characters of the *andra* group have remained consistent with the original diagnosis (García Aldrete 1974), notably, the presence of a distinct pigmented area on the dorsal (internal) surface of the subgenital plate, the presence of four macrosetae in a particular arrangement (Fig. 18) on the subgenital plate, and the valvulae being single, short, rounded distally, bearing few setae, and attached completely or nearly so to the ninth sternum. This set of characters holds the group together. In addition, all but two species examined show the male clunium to paraproct articulation discussed above, and most of the included species have some degree of pigmentation of the forewing membrane, usually in the form of clouding bordering the R, M, and Cu1 veins at the wing margin.

On the basis of male terminal abdominal structures, the *andra* group can be divided into four subgroups as follows.

Subgroup I. Forms with free claspers (i. e. claspers not fused to hypandrium); hypandrium with a thin median distal lobe covering partially the distal end of the phallosome; phallosome a single stem forked posteriorly (ca. three-fifths distance from base to apex), each tine bilobed or trilobed at its apex. Included species: *L. andra* Sommerman, *L. dona* Sommerman, *L. nubilis* (Aaron), *L. nubiloides* García Aldrete, and *L. punctata* (Banks). All are Nearctic.

Subgroup II. Forms with claspers present but fused to the hypandrium; hypandrium with or without a median distal lobe; phallosome a single stem forked in posterior half, each tine terminating in a spearhead-like structure. Included species: *L. arnae* Sommerman, *L. buettikeri* New, *L. dichodolichna* (Li) (= *Dicrolachesillus dichodolichnus* Li; see Lienhard, 2003), *L. kerzhneri* Günther, *L. novemimaculata* Li (= *Dicrolachesillus novemimaculatus* (Li); see Lienhard, 2003), and *L. tanaidana Roesler.* All are Palaearctic except *L. arnae* in western Canada and northwestern USA.

Subgroup III. Forms with hypandrium extended posteriorly as two lateral lobes with no median distal lobe; claspers (?) represented by appendages on or near tips of hypandrial lobes or totally absent; phallosome consisting of two separate rods, or the two rods fused at base. Included species: *L. ambigua* Badonnel, *L. kola* Sommerman, *L. mayorgae* García Aldrete and *L. texana* **n. sp.** *Lachesilla bilobata* García Aldrete, *L. castrii* Badonnel, *L. chiapensis* García Aldrete, and *L. zapoteca* García Aldrete, known only from females, also probably belong here. All are Neotropical except *L. kola* (northern Mexico and southwestern USA), and *L. texana* (Great Smoky Mountains, central and southern Texas, and northern Mexico).

Subgroup IV. Forms with claspers represented by a pair of diagonal lines converging postero-medially on the hypandrium and a spike-like projection at their convergence; hypandrium with two rounded lateral lobes and no median distal lobe; phallosome consisting of two rods fused at base. Included species: *L. falcicula* Badonnel, and *L. sonamarga* García Aldrete, both Himalayan. These two species also differ from the other species of the *andra* group in that the clunial arm to the paraproct extends laterally rather than postero-laterally and the forewing membrane is unmarked. Females of these two species show characters typical of the *andra* group except for lack of wing markings.

The array of species constituting the genus *Zonolachesillus* Li (2002) may also belong in this subgroup. The female characters illustrated for these species (Li, loc. cit., Figs. 1531 E, E; 1532 E; 1533 D, E; 1535 E; 1536 E, G; 1537 G, H; 1539 H, I; 1540 H, I; 1541 I, J, K and 1542 E, F) do not conform with the *andra* group, so their placement remains uncertain.

The *andra* group may be viewed as a clade within the genus *Lachesilla* on the basis of the synapomorphy of the valvulae being reduced and fused distally to the ninth sternum. The presence of an arm on each side of the male clunium extending postero-laterally to an articular region on the paraproct is an apomorphy for subgroups I through III, but is not found in subgroup IV. In the latter subgroup, a short arm of the clunium extends laterally to the articular region of the paraproct. This articulation is also seen in the *centralis, corona, fuscipalpis, mexica, pedicularia, riegeli,* and *texcocana* groups of *Lachesilla* and in the genera *Nadleria* and *Hemicaecilius*. We believe it to be the plesiomorphic state for *Lachesilla.*

The subgroups set out above, though conceived on a phenetic basis, may also be clades. Mockford (1985) hypothesized probable directions of evolution of exoskeletal parts of male external genitalic and paragenitalic structures in *Lachesilla*. The hypotheses were derived from the presumed sister-group relationship between the genera *Nadleria* and *Lachesilla*. Subsequently, this view of phylogenetic relationships has been modified (García Aldrete 2008) such that *Lachesilla* appears to be the sister-group of *Ectolachesilla* García Aldrete, while *Nadleria* and *Hemicaecilius* form a generic pair with a sister-group relationship to the *Lachesilla – Ectolachesilla* generic pair. Since the male of *Ectolachesilla* remains unknown, we must still rely on comparison with males of *Nadleria* and a single damaged male of *Hemicaecilius* sp. (still undescribed) for the interpretation of derivation of male structures in *Lachesilla*. Mockford's (1985) hypotheses concerning directions of evolution in claspers, phallic apodemes, and the hook-like distal paraproctal process appear to remain sound.

In subgroup I, claspers free from the hypandrium and the bilobed or trilobed tines of the phallosomal fork are synapomorphies. In subgroup II, the pointed terminal 'spear-heads' of the phallosome and the elongate, slender claspers may be synapomorphies. In subgroup III, absence of claspers and separation of the phallosomal apodemes into two, fused only at the extreme base, or not at all, are probably synapomorphies (although longer basal fusion of the apodemes may be a plesiomorphy for the *andra* group and even for the entire genus).

Within subgroup III, *L. texana* and *L. mayorgae* form a clade with the following synapomorphies: (1) a series of radial spots in the forewing and (2) P4 very dark. In these two species, the phallosomal apodemes are fused basally. This condition is probably a plesiomorphy in subgroup III. The other five members of the subgroup form a separate clade with the apomorphy of the phallosomal apodemes being separate throughout their length. The details of relationships in this clade are beyond the scope of the present paper.

In subgroup IV, the mode of clunium-paraproct articulation appears to be a plesiomorphy for the *andra* group. The particular mode of reduction of the claspers may be viewed as an apomorphy for the subgroup. It could have led to the lack of claspers of subgroup III, but that seems unlikely in that subgroup IV shows total absence of forewing markings, whereas subgroup III shows a forewing marking pattern typical of the other two subgroups or more extensive.

Key to the subgroups of the *Lachesilla andra* species group (males only)

1 Claspers well developed and not fused to body of hypandrium but separated from it by a distinct line or attached to it at their base by membrane (see García Aldrete, 1974, Fig. 7). Phallosome a single stem forked posteriorly, each tine bilobed or trilobed at its apex ..... Subgroup I

-. Claspers, when present, completely fused to body of hypandrium with no line of separation; claspers often greatly reduced or absent (see Fig. 6 and García Aldrete, 2000, Figs. 3, 10). Phallosome not as above; if a single stem forked posteriorly, then each tine terminating in a spearhead-like structure; otherwise, phallosome either two rods fused only at base, or two separate rods 2

2 Phallosome a single stem forked in posterior half; each tine terminating in a spearhead-like structure ..... Subgroup II

-. Phallosome of two separate rods, or the two rods fused only at base 3

3 Hypandrium extended posteriorly as two lateral lobes (Fig. 6); claspers either absent or represented (?) by a small process on or near the tip of each lateral hypandrial lobe ..... Subgroup III

-. Hypandrium terminating as two rounded lobes not extending posterior to hypandrial midpoint; claspers represented by a pair of diagonal lines across hypandrium, converging at posterior hypandrial midpoint and a small cone or spike-like projection at their point of convergence ..... Subgroup IV

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