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Phymonotus jacintotopos: A new genus and species of shield-backed katydid (Orthoptera: Tettigoniidae: Tettigoniinae: Nedubini) from the San Jacinto Mountains of California, USA

DAVID C. LIGHTFOOT[1], DAVID B. WEISSMAN[2] & NORIHIRO UESHIMA[3]

[1]*Museum of Southwestern Biology, Department of Biology, University of New Mexico, MSC03 2020, Albuquerque, NM 87131 USA. E-mail: dlightfo@unm.edu*

[2]*Department of Entomology, California Academy of Sciences, San Francisco, CA 94118 USA. E-mail: gryllus@gmail.com*

[3]*1435-1 Kubo-cho, Matsusaka, MIE 515-0044, Japan. E-mail: nori-ue@ma.mctv.ne.jp*

Abstract

We describe the monotypic shield-backed katydid genus *Phymonotus* and species *jacintotopos* from the San Jacinto Mountains of southern California, USA. *Phymonotus* is unique in having an unusually enlarged dome-like pronotum, a distinctive song, and seven additional distinctive morphological features. We believe that *Phymonotus* is a Pleistocene relic taxon, now endemic to geographically isolated high elevation conifer forests of the San Jacinto Mountains. Nearest relatives *Agalothorax* and *Neduba* taxa occur in lower elevation environments throughout the surrounding region. *Phymonotus* is a member of the katydid tribe Nedubini which has a Gondwanan distribution with additional taxa in Australia and South America (Chile and Argentina). Western North American Nedubini apparently result from a South American dispersal event. We also describe characters newly used for the description and diagnosis of *Phymonotus*, the dorsal and ventral lobes of the titillators, and the dorsal sclerites of the titillators. We report evidence that *Phymonotus* males may produce thoracic glandular secretions that are offered to mating females.

Key words: *Agalothorax*, calling song, description, dorsal and ventral lobes of the titillators, dorsal sclerite of the titillators, karyotype, *Neduba*, San Jacinto shield-backed katydid, thoracic glandular secretions

Introduction

We here describe the shield-backed katydid *Phymonotus jacintotopos* Gen. et sp. nov. (Figs 1, 2) from southern California. This taxon is a member of the tribe Nedubini Rentz and Colless, which has a world geographic distribution consistent with Gondwanan origins. Most species occur in Australia (Eades *et al*. 2011: 13 genera and 50 species), others in South America (Eades *et al.* 2011: 5 genera and 21 species), and a geographically disjunct group of three genera, including *Phymonotus*, in western North America. *Phymonotus* is most closely related to the other North American Nedubini genera *Agalothorax* Caudell (5 species) and *Neduba* Walker (9 species). Other researchers (Rentz and Colless 1990, Cole 2009, 2010) included *Phymonotus* as an unnamed taxon in morphological and molecular phylogenetic analyses, respectively, and found *Phymonotus* to be a distinct taxon equivalent to the genus rank, sister to *Agalothorax* and *Neduba*. We concur with that phylogenetic placement, and provide a formal description. Also, we name and describe new morphological characters; the dorsal sclerite of the titillators, which is unique to *Phymonotus*, and the dorsal and ventral lobes of the titillators, which are present in all three genera, but differ among the genera relative to sclerotized structures. We report evidence that *Phymonotus* males may produce thoracic glandular secretions for mating females, which is unknown among other Tettigoniinae.

Material and methods

Specimens of *Phymonotus*, *Agalothorax* and *Neduba* were borrowed from the California Academy of Sciences, San Francisco, CA (CAS) and the Museum of Southwestern Biology, University of New Mexico, Albuquerque,

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NM (MSB). The late E. R. Tinkham possessed a large series of *Phymonotus* from around the type locality of Idyllwild, CA, collected in the 1960's. We viewed those specimens in the 1980's. After his death in 1987 (Weissman 1988), those specimens were not located, but we cite some of his notes.

Morphological features were measured with an ocular micrometer on an American Optical Spencer® stereo step-zoom dissecting microscope. Anatomical features were photographed with a Nikon D200 camera and 60 mm macro lens, and a Visionary Digital® micro-photographic system with an Infinity® K2 microscopic lens, along with Helicon Focus® imaging software. Figure images were prepared with Adobe Photoshop CS3® software. Testes were removed from live males and fixed in 3 parts 100% ethanol: 1 part glacial acetic acid, and examined by squash technique. Calling songs were recorded by a Uher 4000 Report IC and subsequently digitized at a sample rate of 44,100/s and analyzed with CoolEdit 2000 (Syntrillium Software).

Phymonotus Lightfoot, Weissman and Ueshima new genus

Type species. *Phymonotus jacintotopos* Lightfoot, Weissman and Ueshima, here designated.

Diagnosis and description. See Table 1. Known only from San Jacinto Mountains, Riverside Co., California (Fig 3). As with other Nedubini world-wide, *Phymonotus* males possess modified and enlarged paraprocts, or pseudocerci, that extend posteriorly from beneath the supra-anal plate or tergum 10, and which function as clasping organs (Rentz and Colless, 1990). The supra-anal plate, or epiproct, of *Phymonotus* males is unique among North American Nedubini in that it is hour-glass shaped. *Phymonotus* is most similar and closely related to the endemic North American genera *Agalothorax* and *Neduba*, and can be separated from the latter two genera by a combination of characters presented in Table 1, including obvious features such as a dome-shaped metazona, two lateral lobes on each side of the pronotum, concave posterior margin of the metazona, calling song, and the apical indentation of the female subgenital plate. As with *Agalothorax* and *Neduba*, *Phymonotus* possesses an enlarged metazonal pronotal disk relative to other Tettigoniinae genera. However, in *Phymonotus* this disk is uniquely shaped, being considerably dorsally elevated and dome-shaped with a concave posterior margin. The dome of the metazona of *Phymonotus* includes both the dorsal disk and the lateral lobes, and is more pronounced in males than females. The height of the metazona in adult male *Phymonotus* averages 1.6 times the height of the prozona, while the height of the metazona in female *Phymonotus* and both sexes of *Neduba* and *Agalothorax* is close to equal to the height of the prozona. The pronotum of *Phymonotus* males has two lateral lobes, one on the prozona, and another on the metazona, unlike *Agalothorax* and *Neduba* males that have one lateral lobe shared by both the prozona and metazona. We name and describe the male dorsal and ventral lobes of the titillators (referenced as fleshy lobes but not named by Rentz and Gurney (1985)), and the dorsal sclerites of the titillators (see species description below). All three genera possess both dorsal and ventral lobes of the titillators. The dorsal lobes of the titillators in *Agalothorax* and *Neduba* are simple soft membranes that lack dorsal sclerites. In contrast, *Phymonotus* possesses dorsal sclerites of the titillators, which are developed as a sclerotized bi-lobed structure on the dorsal lobes of the titillators. All three genera possess ventral lobes of the titillators. In *Agalothorax* the ventral lobes possess sclerotized teeth, and in *Neduba* the ventral lobes possess ventral sclerites (Rentz and Birchim 1968). In contrast, *Phymonotus* lacks any sclerotized structures on the ventral lobes of the titillators.

Phymonotus jancintotopos Lightfoot, Weissman and Ueshima new species

Figures 1, 2, 3, 4, 5, 6, 7, 8; Tables 1, 2.

Holotype. Male. (Figs 1a, b) USA, California, Riverside County, San Jacinito Mountains, Fern Valley, Idyllwild, intersection of Fern Valley Road and Dickinson Road N 33° 45' 22.39" W 116° 41' 59.21", 1,767 meters elevation, 31 August 1986, coll. D.B. Weissman, B.I. Weissman, D.C.F. Rentz, DBW stop number S86-105, song recording number R86-202, testes preserved for chromosome analysis sample number T86-86. Type deposited in CAS, number18565.

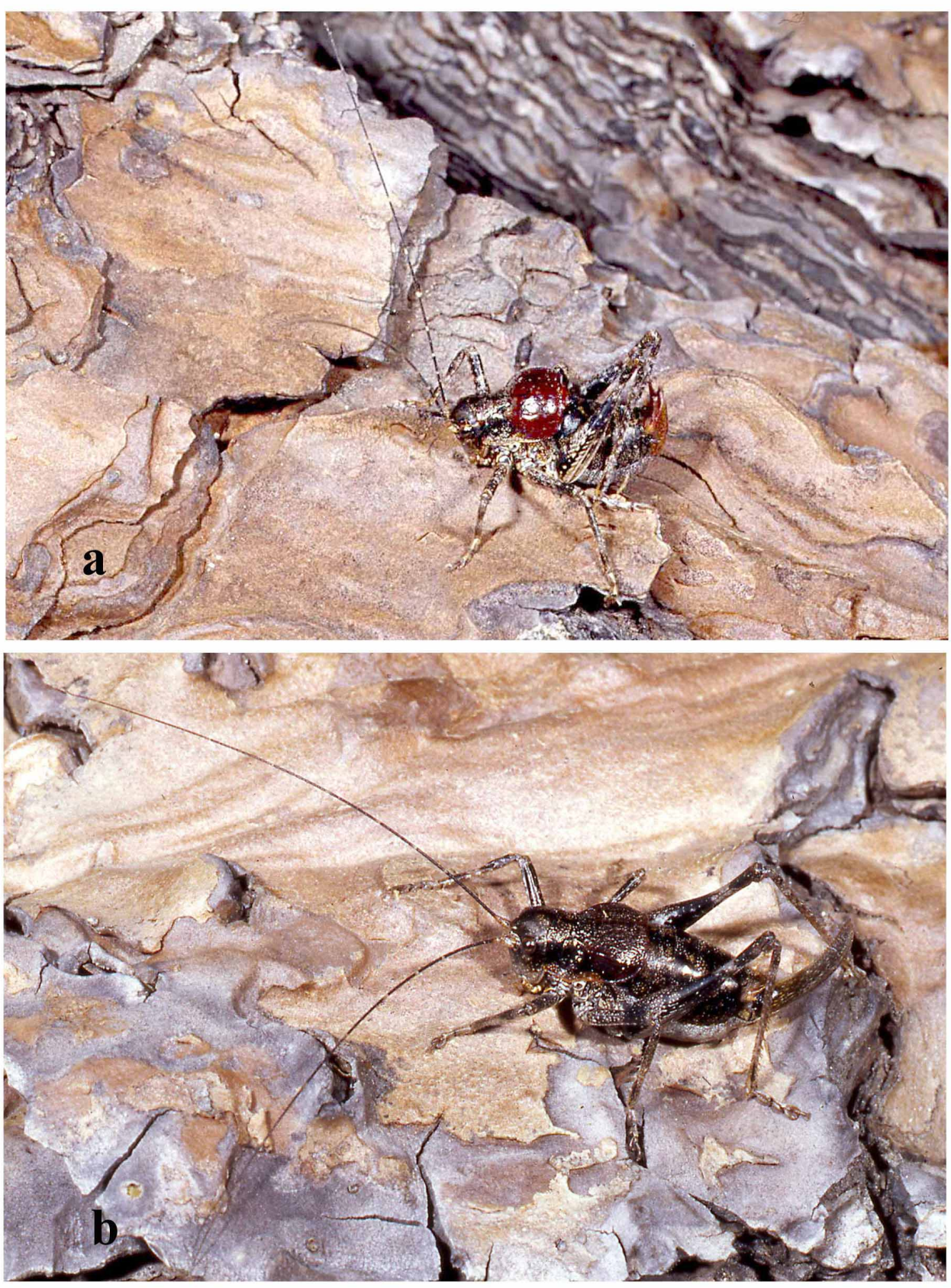

FIGURE 1. Live male (a) and live female (b) paratypes of *Phymonotus jacintotopos* **gen. et sp. nov.** on Jeffery pine bark at the type locality.

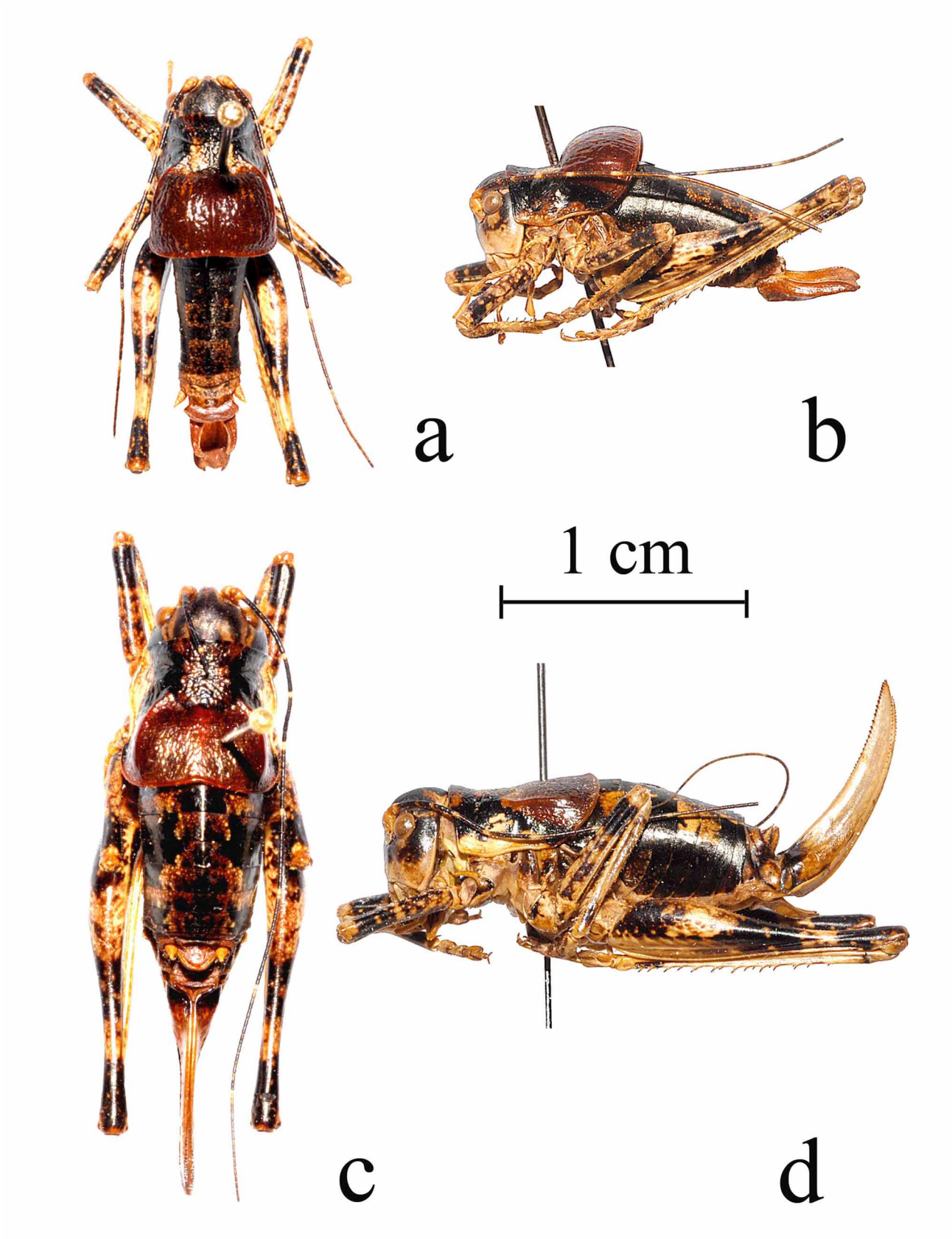

FIGURE 2. a. Dorsal view of *Phymonotus jacintotopos* **gen. et sp. nov.** male holotype; b. lateral view of male holotype; c. Dorsal view of female paratype; d. lateral view of female paratype.

Paratypes: USA: California: Riverside Co: Fuller Mill Creek nr. Idyllwild, 6 September 1969, coll. P. Rauch, S. Larish, 1♂ (in ethanol), CAS; trail above Idyllwild, elev. 5,500 ft., 25 December 1969, coll. J. Emmel, O. Shields, 3♂, CAS; Idyllwild; elev. 1,950 m, 12 December 1982, coll. K.W. Cooper, 1♀, CAS; San Jacinto Mountains, Idyllwild, 27 August 1983, coll. S. Bennett, DBW stop number S83-120, 1♀, immature, (CAS); San Jacinto Mountains, Cinco Poses Springs, elev. 7,200 ft, 4 September 1985, on ponderosa pine trees, coll. D. Goodward, 2♂, 2♀, CAS; San Jacinto Mountains, intersection of Fern Valley & Dickinson Roads, elev. 5,900 ft, 31 August 1986, coll. D.B. Weissman, B.I. Weissman, D.C.F. Rentz, DBW stop number S86-105, song recordings R86-105, R86-192, R86-196, R86-202, R86-203, R86-206, R86-219, R86-120, testes preserved for chromosome analysis T86-81, T86-82, T86-86, T86-87, T86-90, T86-91, T86-92, 12 ♂ (including holotype), 12♀, CAS; Boulder Basin Campground,15 mi NW of Idyllwild, 33.826º N, 116.755º W, elev. 2,498 m, 6 October 2001, coll. J.A. Cole, 7♂, 1♀, MSB; San Jacinto Mountains, Idyllwild, intersection of Fern Valley & Dickinson Roads, N 33° 45' 22.39" W 116° 41' 59.21", elev. 1,767 m, 31 August 2005, on Jeffery pine trees, coll. D.B. Weissman, D.C. Lightfoot, DBW stop number S05-114, 1♂, 1♀, MSB.

Diagnosis. Monotypic. See Table 1 and diagnosis for the genus *Phymonotus* to distinguish *P. jacintotopos* **gen et sp. nov.** from nearest relatives.

TABLE 1. Comparative character states for *Neduba*, *Agalothorax*, and *Phymonotus* that differentiate genera of North American Nedubini. *Phymonotus* is unique for characters marked with an asterisk.

Character	Gender	Neduba	Agalothorax	Phymonotus
Lateral lobes* of pronotum	both	one	one	two
Metazona* dorsal shape	both	flat	flat	dome
Metazona * posterior dorsal margin	both	acute	acute	concave
Supra-anal* plate shape	male	quadrate	oval	hour-glass
Titillator arms	male	robust, not diverging	sinuous, diverging	sinuous, diverging
Base of* Titillator	male	sclerotized	sclerotized	not sclerotized
Dorsal sclerite of titillator	male	absent	absent	present
Ventral sclerite* of titillator	male	present	absent, but teeth present on ventral lobe	absent and no teeth on ventral lobe
Calling song*	male	continuous, with several pulse types	single pulses with short intervals	single pulses with long intervals
Subgenital plate	female	no spiniform appendages	Spiniform appendages	no spiniform appendages
Subgenital* plate	female	no apical indentation	no apical indentation	Apical indentation

* Character states unique to *Phymonotus*.

Etymology. The genus name *Phymonotus* is the Greek prefix "*phymo*" for swollen, and the Greek suffix "*notum*" in recognition of the unusually enlarged, dome-shaped pronotum. The species name *jacintotopos* is composed of "*Jacinto*" for the Spanish name of the San Jacinto Mountains, and the Greek suffix "*topos*" for place, recognizing the San Jacinto Mountains, where the genus and species are endemic. Pronounced in English "haw-sin-toe-toe-pose." We recommend the common name: "San Jacinto shield-backed katydid."

Description. General (Figs 1, 2). Body robust, size medium compared to other North American Tettigoniinae, similar in size and build to other Nedubini, brachypterous. Body lengths of males 13.7–18.2 (15.5) mm (holotype male measurements in parentheses, see Table 2 for average measurements) and body lengths of females 13.5–20.9 mm. Females are generally larger than males, except for the dimensions of the metazona, which are larger in males.

Head (Fig 2). Frons flat, weakly oblique, smooth and shiny, mid-dorsally acute and raised anteriorly to a rounded point between the eyes, equal in height to the height of the sclerotized base of the antennal socket above the circumantennal sulcus; gena smooth, shiny, and broadly rounded; basal width of dorsal head margin 3.9–5.5 (4.8) mm in males, and 4.0–5.7 mm in females. Dorsal head length from posterior margin to anterior tip of vertex

1.7–2.8 (2.1) mm in males, and 1.8–3.3 mm in females; anterior apex of vertex elevated to the height of the antennal scape folded back against the head, gradually lowering to the occiput and posterior margin of the head; width of vertex between the eyes 0.5–0.7 (0.5) mm in males and 0.5–0.8 mm in females, fastigium oval and concave anteriorly, forming a shallow depression, rounded anteriorly, and acute posteriorly, equal in width to the antennal pedicel; slightly broader and shallower in females than males; top of head with dull, smooth surface, distance between the eyes 2.2–2.8 (2.6) mm in males and 2.2–3.2 mm in females; eye round, slightly extended subanteriorly when viewed laterally, ventral/dorsal height 1.1–1.3 (1.3) mm in males and 1.2–1.6 mm in females, and anterior to posterior width 1.0–1.2 (1.2) mm in males and 1.0–1.4 mm in females; ocelli absent. Antennae filiform, about 1.5 times the body length (Fig 1).

TABLE 2. *Phymonotus jancintotopos* **gen. et sp. nov.** morphological measurements in millimeters, measured from 15 female and 24 male adult paratype specimens, and from the male holotype. See species' description text for holotype measurements in parentheses. See Appendix 1 for details on how measurements were taken.

Morphological Feature	Male			Female		
	Average	Maximum	Minimum	Average	Average	Minimum
Body Length	15.74	18.20	13.69	18.48	20.88	13.53
Head Width	4.52	5.48	3.90	5.13	5.73	3.98
Head Length	2.24	2.82	1.74	2.67	3.32	1.83
Head Vertex Width	0.58	0.67	0.50	0.68	0.84	0.46
Eye Width	1.08	1.18	0.97	1.19	1.39	1.01
Eye Height	1.24	1.34	1.13	1.37	1.55	1.18
Inter-eye Distance	2.53	2.82	2.24	2.86	3.24	2.24
Prozona Length	2.49	2.91	2.07	2.91	3.57	2.32
Prozona Dorsal Width	2.01	2.49	1.58	2.27	2.49	1.83
Prozona Ventral Width	5.62	6.47	4.81	6.22	7.06	4.90
Prozona Depth	2.61	3.07	2.07	2.98	3.57	2.49
Metazona Length	4.37	5.48	2.74	3.43	3.98	2.66
Metazona Dorsal Width	5.80	6.81	4.40	5.77	6.56	4.57
Metazona Ventral Width	6.27	7.05	5.64	6.65	7.39	5.31
Metazona Depth	4.03	4.90	3.24	3.04	3.65	2.24
Subgenital Plate Length	5.10	5.64	4.23	3.08	3.57	2.08
Subgenital Plate Width	2.21	2.74	1.66	2.80	2.99	2.49
Hind Femur Length	12.75	14.53	10.02	14.33	16.03	10.69
Hind Femur Width	2.61	3.24	2.08	2.91	3.24	2.08
Wing File Length	3.44	3.90	3.10	NA[4]	NA	NA
Wing File Tooth Count	90.9	111.0	81.0	NA	NA	NA
Ovipositor Length	NA	NA	NA	10.84	12.36	8.68
Ovipositor Width	NA	NA	NA	2.46	2.74	2.16
Ovipositor Teeth Dorsal[1]	NA	NA	NA	26.2	38.0	15.0
Ovipositor Teeth Middle[2]	NA	NA	NA	20.5	27.0	12.0
Ovipositor Teeth Ventral[3]	NA	NA	NA	16.0	21.0	13.0

[1]Teeth along dorsal margin of dorsal valve; [2]Teeth along ventral margin of dorsal valve; [3]Teeth along ventral margin of ventral valve; [4]The measurement does not apply, wrong gender.

Thorax (Fig 2)**.** Prozona of pronotum relatively flat on dorsal surface, upcurved along anterior dorsal margin, and strongly upcurved posteriorly toward the metazona, dorsal anterior margin of prozona slightly concave at median, entire margins of prozona represented by a carina throughout, ventral margin of prozona flared outward

laterally, and forming a prozonal lateral lobe, distinct from the metzonal lateral lobe, dorsal length of prozona 2.1–2.9 (2.8) mm in males and 2.3–3.6 mm in females, dorsal width of prozona 1.6–2.5 (2.1) mm in males, and 1.8–2.5 mm in females, ventral width of prozona 4.8–6.5 (5.9) mm in males, 4.9–7.1 mm in females, dorsal to ventral depth of prozona 2.1–3.1 (2.7) mm in males, 2.5–3.6 mm in females, dorsal lateral carina absent on most of prozona, but abruptly appearing posteriorly, and extending to the metazona, principal anterior lateral sulcus of prozona narrow and shallow dorsally, becoming very deep and broad laterally to the ventral margin, secondary posterior lateral sulcus of prozona absent dorsally, shallow below lateral carina, extending ventrally forward and converging with principal sulcus above ventral margin of prozona, forming a slightly concave lateral face of the prozona mid-way to the ventral margin, above the lateral lobe, lateral margin of dorsal surface of prozona with a single to several flat tubercles present on posterior margin of principal lateral sulcus, surface of prozona rugose and shiny; metazona greatly inflated and produced dorsally as a rounded bulbous dome, encompassing both the dorsal disk and the lateral lobe, especially in males, averaging 1.5 times the height of the prozona, less so in females, averaging nearly equal to the height of the prozona; lateral lobe of metazona distinct from the prozonal lateral lobe; posterior margin of metazona strongly and broadly concave, especially in males, metazona dorsal length 2.7–5.5 (4.5) mm in males, 2.7–4.0 mm in females, metazona dorsal width 4.4–6.8 (5.9) mm in males and 4.6–6.6 mm in females, metazona ventral width 5.6–7.1 (6.3) mm in males and 5.3–7.4 mm in females, dorsal to ventral depth of metazona 3.2–5.0 (4.0) mm in males and 2.2–3.7 mm in females, dorsal median carina of metazona pronounced and entire, but only slightly elevated, lateral carina of metazona pronounced, entire, and slightly elevated, terminating just before the intersection with the posterior margin, outer margins of metazona with numerous slightly elevated carina throughout, converging with the same carina of the prozona margin, surface of metazona shiny with numerous anterior/posterior oriented low rugose ridges on dorsal disc and lateral margins; prosternum narrow and U-shaped with one broad spine on each side inside of the front coxae; mesosternum and metasternum both rectangular, with upturned lateral margins just inside of the middle and hind coxae respectively.

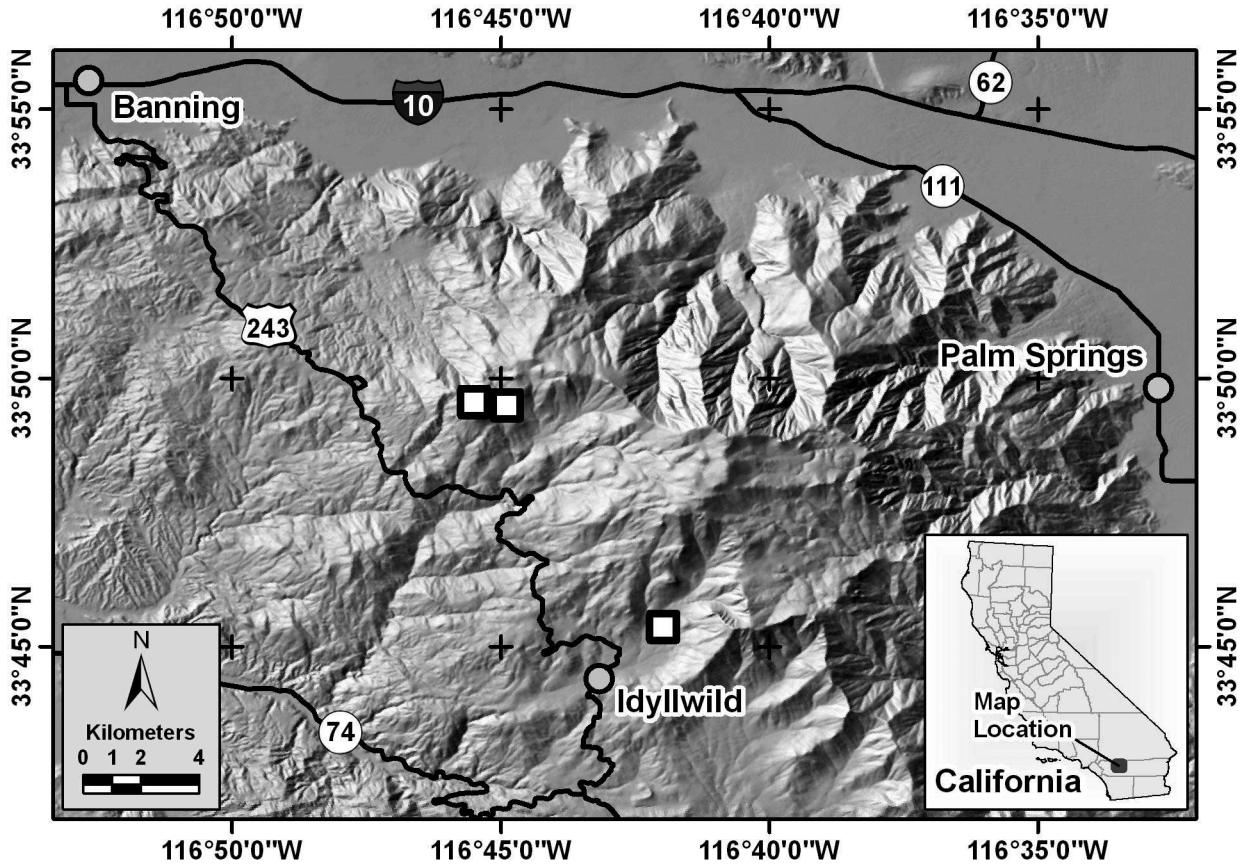

FIGURE 3. Map of the San Jacinto Mountains, Riverside Co., in southern California, open squares (□) marking the known localities of *Phymonotus jacintotopos* Gen. et sp. nov. The southern-most location is the type locality.

Wings (Fig 4). Brachypterous, wings hidden under the pronotal disk (Figs 4a, b); stridulatory file of male wide and straight in the anterior half, curving laterally and tapering to a point in the posterior half (Figs 4b, c), 3.1–3.9 (3.4) mm long; all teeth similar in thickness, but becoming narrow in the posterior portion; tooth count ranging from 81–111 (85).

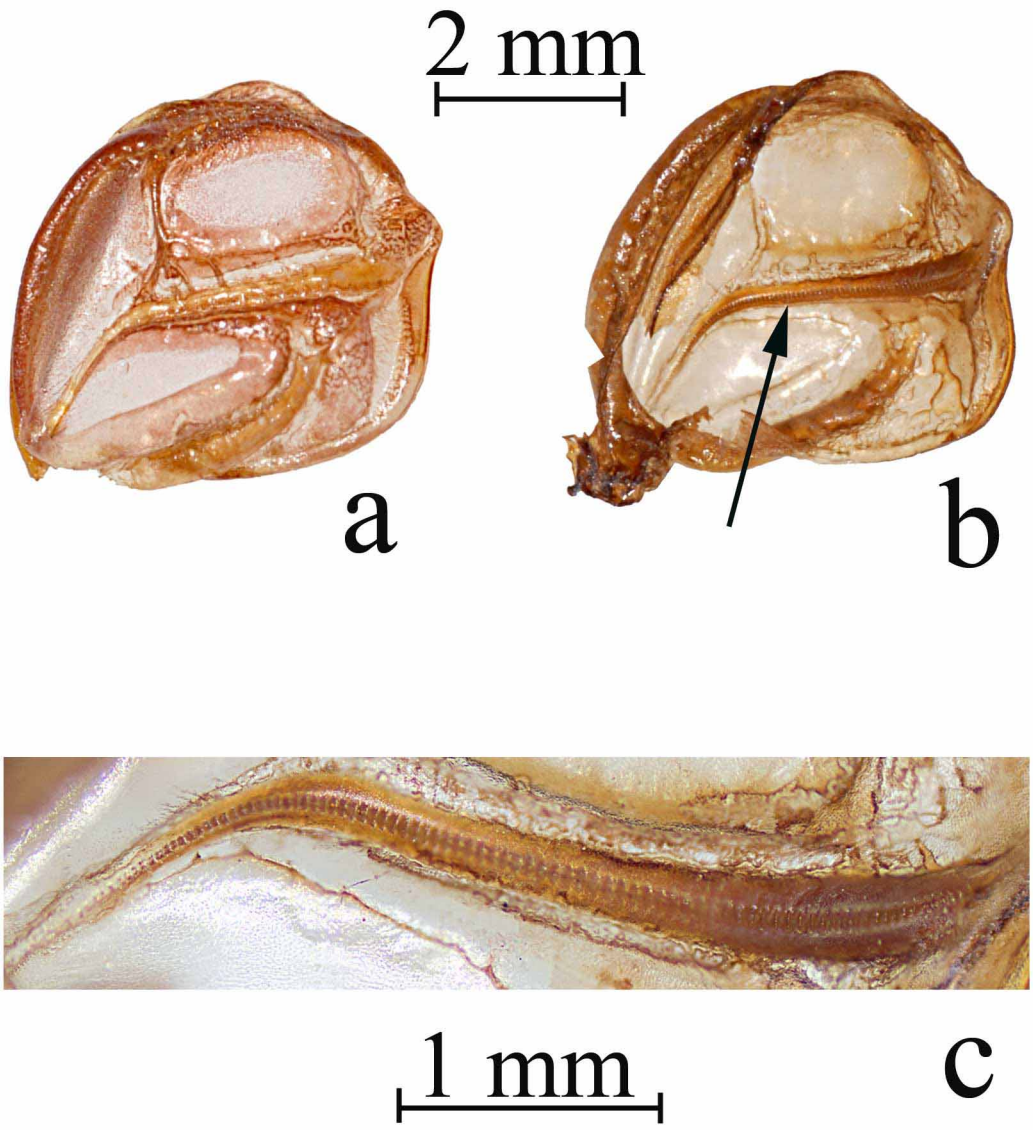

FIGURE 4. Wing of male *Phymonotus jacintotopos* **gen. et sp. nov.**: a. dorsal view; b. ventral view showing stridulatory file (arrow); c. Stridulatory file and teeth.

Legs (Fig 2)**.** Front coxa with a large broad tooth on anterior base pointing downward, middle and hind coxa simple with no armature or extensions. Tympanum on front tibia beneath two narrow longitudinal lateral openings on external and internal margins; front tibia with 6 short spines on both ventral margins, one spine on outer margin at apex, and one spine on middle dorsal margin above the tympanum; front femur with one very small spine on inner ventral margin at apex; middle tibia with 7 short spines on both ventral margins, 3 short spines on both dorsal margins; hind tibia with 13 short spines on both dorsal margins, 5 short spines on both inner and outer ventral margins, and one large apical spin on both inner and outer lateral margins; hind femur length of males 10.0–14.5 (13.9) mm in length, and 2.1–3.2 (2.9) mm in width, hind femur of females 10.7–16.0 mm in length and 2.1–3.2 mm in width, with series of small teeth along the dorsal surface of the dorsal valve near the apex, a series of small teeth on the ventral surface of the ventral valve near the apex especially near the middle 1/3.

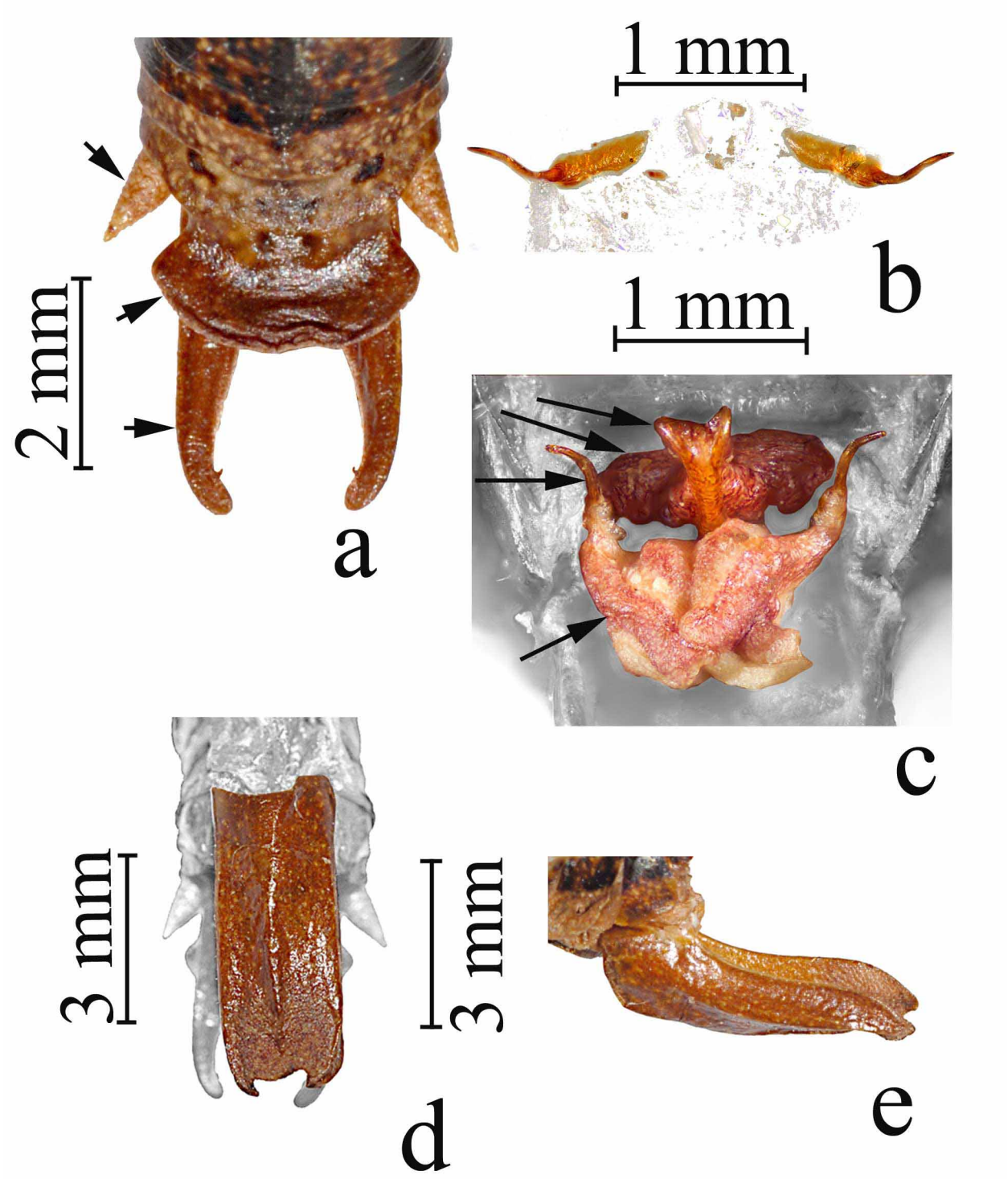

FIGURE 5. a. Apex of male *Phymonotus jacintotopos* **gen. et sp. nov.** abdomen, dorsal view, showing cercus (top arrow), supra-anal plate (middle arrow) and paraproct (bottom arrow); b. Male titillators dissected from abdomen, dorsal view; c. Male dorsal lobe of the titillators (arrow second from top), supporting the scelrites of the titillators (top arrow), apex of the left titillator arm (arrow third from top), and ventral lobe of the titillator (bottom arrow), background gray-tone area showing supra-anal plate on top and subgenital plate on bottom. Note that the dorsal and ventral lobes of the titillators are dry and withered on the pinned specimen illustrated, while they are full and turgid in live specimens; d. Male subgenital plate, ventral view, background gray-tone showing ventral view of apex of male abodomen; e. Male subgenital plate, lateral view.

Abdomen (Figs 2, 5, 6)**.** Cercus short, simple styliform (Fig 5a); supra-anal plate (epiproct) of male large, broad basally, constricted medially, and then broad again distally, forming an hour-glass shape, and dorsally cover-

ing the basal 2/3rds of the paraprocts beneath (Fig 5a); supra-anal plate of female broadly triangular, broadest basally (Fig 6a); paraprocts of male long, narrow and dorsal/ventrally flattened, broad basally, narrowing to a rounded apical point that is strongly incurved with a small stout tooth located interior just below the apex (Fig 5a); titillator of male simple, arm sclerotized, slender and cylindrical, tapering to dorsal-laterally divergent apical point relative to the other titillator arm, sclerotized titillator arm separated from the right titillator arm by a non-sclerotized membranous base that is subequal to the length of a single arm (Fig 5b); we here name and describe the dorsal and ventral lobes of the titillators, and the dorsal sclerites of the titillators, all located between the supra-anal and subgenital plates (Fig 5c, colored features, gray background areas are the supra-anal and subgenital plates), the dorsal lobe being fleshy basally (Fig 5c, second arrow from top) (note that the dorsal lobe illustrated is dry and withered, it is full and turgid in live specimens) and supporting a sclerotized lobed structure that we name the dorsal sclerite of the titillator (Fig 5c, top arrow), projecting dorsally and anteriorly above the titillator (Fig 5c, third arrow from top shows apical tip of the left titillator arm); a ventral sclerite of the titillator as in *Neduba* is lacking, instead represented only by a fleshy lobe (Fig 5c, bottom arrow) that we here name the ventral lobe of the titillator (note that the ventral lobe illustrated also is dry and withered, it is full and turgid in live specimens); subgenital plate of male elongate and rectangular, 4.2–5.6 (5.6) mm long, and 1.7–2.7 (2.2) mm wide, concave ventrally, deepest in middle (Fig 5d, e), ventral face with strong lateral carinae straight until apex with apical portions incurved with one small apical tooth on each side, median ridge of ventral face straight throughout, anterior margin acute, posterior margin broadly emarginate between the incurved ends of the lateral carinae (Fig 5d, e); subgenital plate of female (Fig 6a) triangular, 2.1–3.6 mm long and 2.5–3.0 mm wide, broad across anterior margin and tapering to a rounded point on posterior margin, anterior lateral lobes rounded, median 1/3 elevated from anterior to posterior margins, with a longitudinal central groove throughout, deepest in the posterior portion, anterior margin down curved ventrally, posterior margin not curved, posterior apex narrowly emarginated forming a V-shaped indention (Fig 6b); female ovipositor shorter than hind femur, 8.7–12.4 mm long, at base, and 2.2–2.7 mm wide at base, laterally flattened, and tapering to apical point, upturned throughout, but abruptly upturned about 2/3 the distance from the base (Fig 6c), row of 15–38 small regularly spaced teeth on dorsal margin up upper valve beginning at mid-distance from base to the apex, row of 12–27 teeth on ventral margins of upper valves beginning about 3/4 the distance from base to, row of 13–21 teeth on ventral margin of lower valves beginning about 4/5 the distance from the base to the apex, no teeth on dorsal surface of lower valves, both upper and lower valves with a tooth at the apex (Fig 6c).

Coloration (Figs 1, 2)**.** Overall coloration varies from individuals that are largely black dorsally, to individuals that are largely brown to tan dorsally, metazona always reddish-brown; head uniformly black to brown dorsally above eyes and antennae, except for light brown patches on either side of the posterior margin of the occiput, those patches much larger and linear, extending laterally along the vertex to the posterior margin of the occiput, pale individuals have a large tan patch posterior to the eye, below the eye becoming dark brown to light brown with scattered tan to whitish dots on the frons and gena, lighter brown to tan on the clypeus and labrum, also with scattered tan or whitish dots; eye black to dark brown with lighter mottling; palps tan; scape and pedicel of antenna tan, flagellum dark brown to black, with repeated banding pattern of single or double whitish segments at intervals of about every 5–7 segments on the basal half of the flagellum, to intervals of 8–10 segments on the apical half of the flagellum; pronotum black to brown on dorsum of prozona, side of prozona also black to brown dorsally, with black patch along the lateral shoulder, posterior margin and lateral lobe of prozona abruptly becoming tan to whitish and extending up to the anterior base of the metazonal lateral carina creating a triangular light mark, metazona uniform dark to light reddish-brown dorsally throughout, anterior portion of metazona lateral lobe often tan to whitish near anterior ventral margin, and often black on lateral lobe from lateral margin mid-way to the lateral carina; remainder of thorax black to brown with considerable tan to whitish maculations, sternal plates light brown to tan with some lateral brown mottling and considerable mottling of whitish dots; wing pads uniform pale brown to tan; fore and middle legs generally a mix black or brown with considerable mottling of tan to whitish dots, especially on the femora, spines and teeth pale brown or tan basally, and black or brown apically; hind femora dorsal surface black to brown, mottled with tan to whitish dots, a heavy concentration of light mottling forming a large tan to whitish patch across the lateral and dorsal surface about 1/5th the distance from the base, and another light band on the narrowest portion of the femur about ¼th the distance below the apex, the size of those light patches much larger in pale individuals, ventral surface of hind femora tan, hind tibia uniform brown to tan, usually with dark brown or black maculations, spines and teeth, pale brown or tan basally, and black or brown apically; abdomen black to brown dorsally, tergites 5–8 with patterns of tan to whitish mottling only in dark individuals, but usually

forming quadrate to ovoid tan or whitish medio-lateral markings on tergites 5 and 6, the largest of which occurs on tergite 6, in pale individuals the markings appear on the dorsal surfaces of all tergites, lateral bases of tergites with considerable mottling of whitish dots; sternites uniform reddish brown lightly patterned with whitish dots; supra-anal and subgenital plates of males and females usually uniform reddish brown to light brown, occasionally lightly patterned with whitish dots, paraprocts of male uniform reddish brown, female ovipositor usually reddish brown, varying to tan or pale brown, lightly streaked with whitish markings, basally black or brown, teeth black or brown.

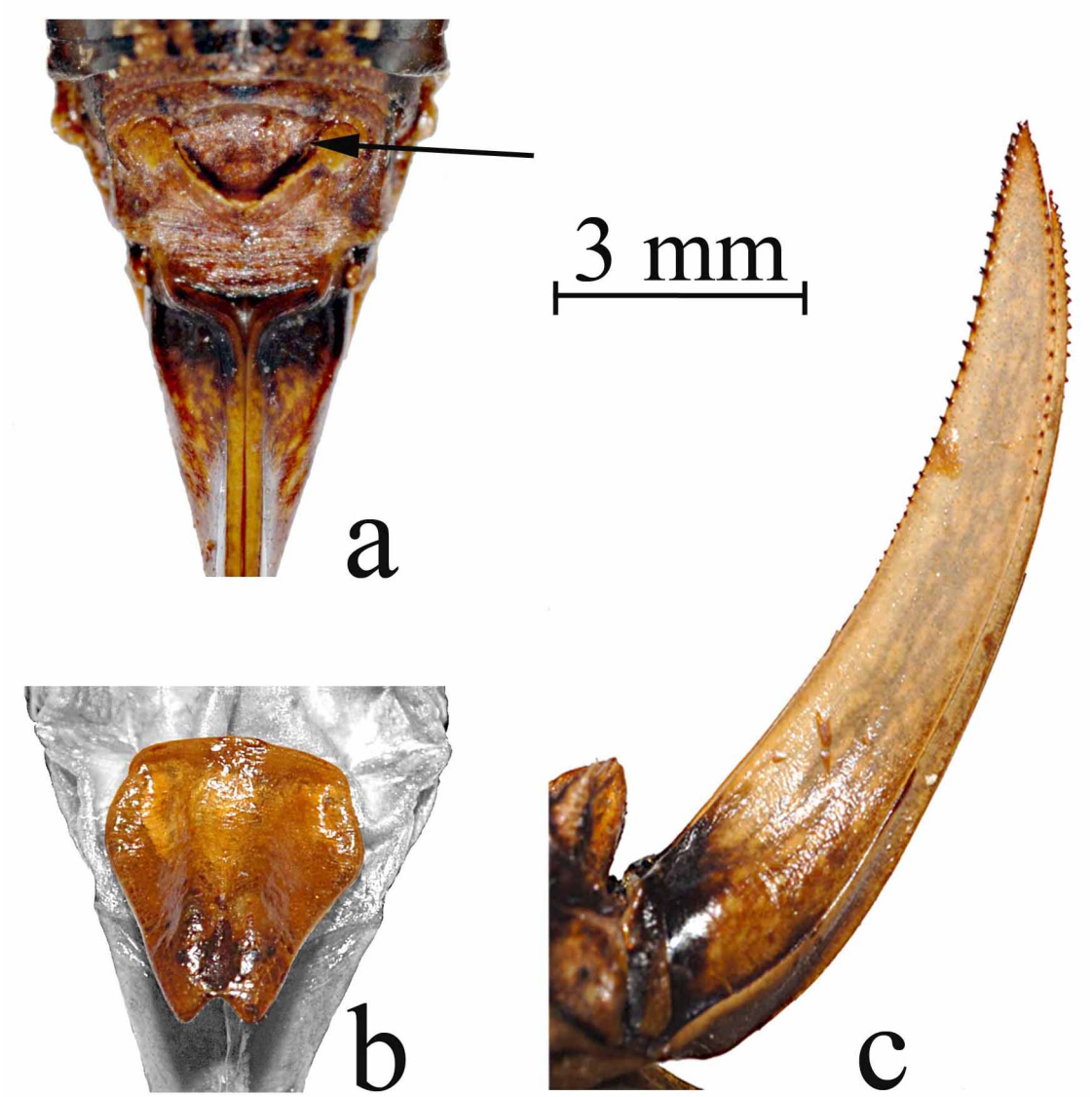

FIGURE 6. a. Dorsal view of female *Phymonotus jacintotopos* **gen. et sp. nov.** supra-anal plate (arrow) and base of ovipositor; b. Female subgenital plate, background gray-tone showing ventral view of apex of female abdomen; c. Female ovipositor, lateral view, note teeth on margins of valves near apex.

Measurements. See Table 2 for values of all morphological characters measured, including the minimum, maximum and average, for both males and females. See Appendix 1 for an illustrate guide as to where measurements were taken on specimens.

Karyotype (Fig 7). 2n♂ =24(22t + XtYt), consisting of 11 pairs of medium to small telocentric autosomes, a very large telocentric X chromosome and a small telocentric Y chromosome (Figs 7a [idiogram], b [mitosis]). First metaphase shows 11 autosomal bivalents and a consistently associated large X and small Y (Fig 7c), and at first anaphase with 11 autosome halves with X at top pole and 11 autosome halves and Y at the bottom pole (Fig 7d). Seven males analyzed.

Calling song (Fig 8). The calling song of *P. jacintotopos* consists of single “swick” pulses with intervals of between 0.8 and 1.0 seconds between pulses at temperatures of 23–25 C (Fig 8a). In the field these swicks are usu-

ally delivered much more slowly since the ambient temperature is much lower. Fig 8b displays a 40X magnification of the 5th pulse showing 9 units, which probably represent individual tooth strikes. These tooth strikes are produced at an average rate of 286 per second. The number of units in the 8 swicks shown in Fig 8 ranged from 7 to 10 with unit rates varying from 231 to 286 per second. If these units are tooth strikes, that is surprisingly few teeth used considering that males average 91 teeth in the file (Table 2). We believe that a combination of pronotal shape and "broadcasting properties," combined with infrequent pulses, results in singing males being extremely difficult to triangulate in the field.

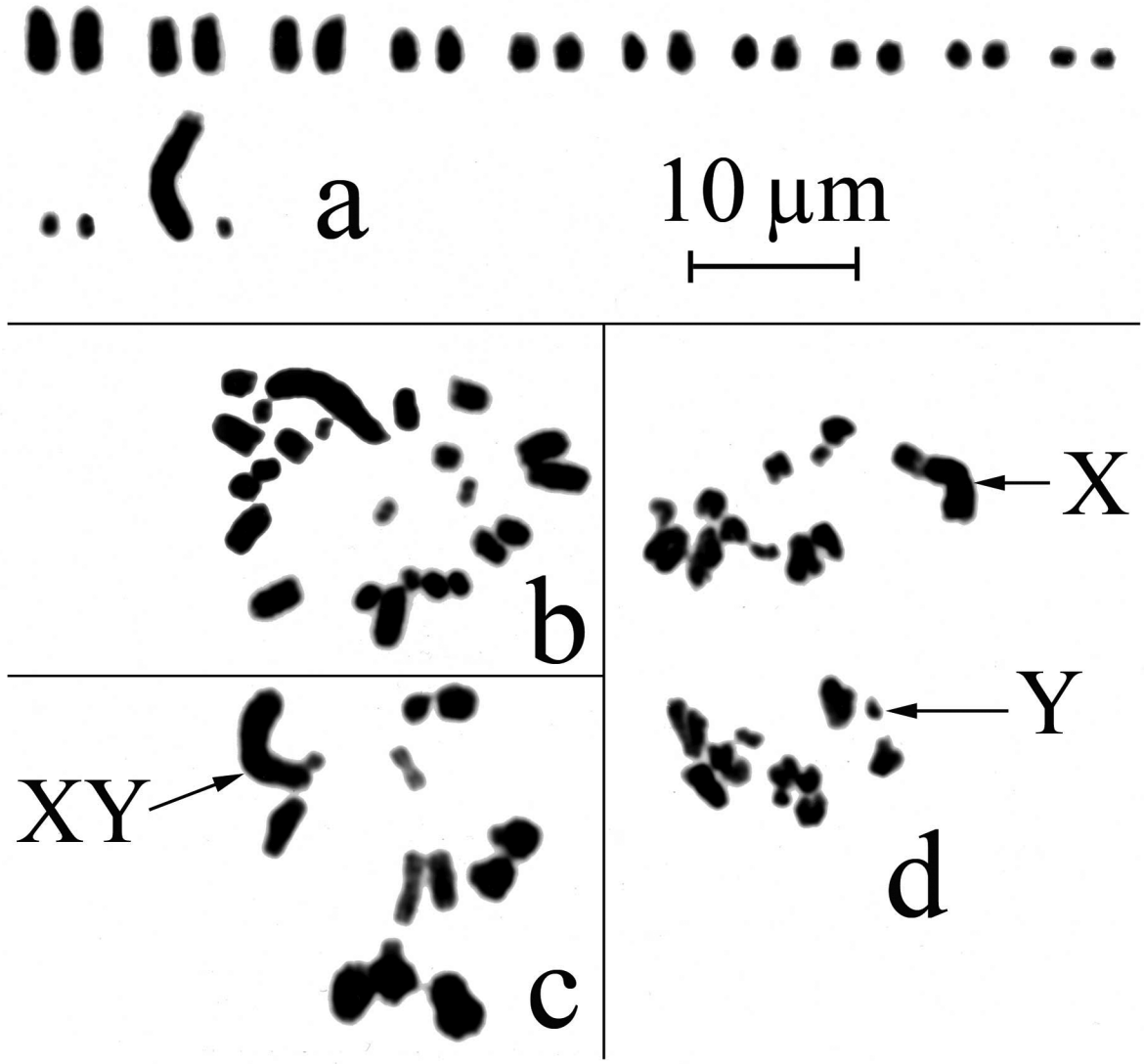

FIGURE 7. Karyotype of *Phymonotus jacintotopos* **gen. et sp. nov.** See text for explanation and note "association" in Fig 7c (arrow) of X and Y sex chromosomes assuring segregation to opposite poles during anaphase one of meiosis.

Natural history. *P. jacintotopos* appears to have one generation per year with adults known from August through January. *Phymonotus* appears to be arboreal and closely associated with conifer trees, especially Jeffery (*Pinus jefferyi)* and Ponderosa (*Pinus ponderosa*) pines in montane mixed-conifer forests composed of Jeffery and ponderosa pine, white fir (*Abies concolor*) and incense cedar (*Libocedrus decurrens*). The body coloration and patterns of *Phymonotus* provides camouflage on the bark of Jeffery pine (Fig 1) and other conifer trees. The type series was collected mainly from ground covering *Vinca* (periwinkle) in a landscaped residential yard beneath a Jeffery pine forest over-story. During a second visit to the type locality, many individuals were heard calling from the pine trees, and none were found near the ground. In natural situations individuals have been found almost exclusively in tree canopies and on tree trunks high above the ground where their mottled dark reddish-brown col-

oration provides good camouflage. The stout, toothed ovipositor of the female may be used to oviposit into bark, as Rentz and Birchim (1968) suggest for *Neduba* and *Agalothorax*. E. R. Tinkham (field notes) kept live adults in captivity and noted that they readily fed on the needles of both Jeffery and ponderosa pine, and on the foliage of incense cedar. *P. jacintotopos* appears to be adapted to cool temperatures as males have been heard calling on cold nights, and have been collected in early January while snow was on the ground and ambient temperatures near freezing (E. R. Tinkham, field notes). Males may also call during the day late in the season when night temperatures are apparently too cold. We found *P. jacintotopos* to be common in Fern Valley, where many individual males could be heard calling from trees at night.

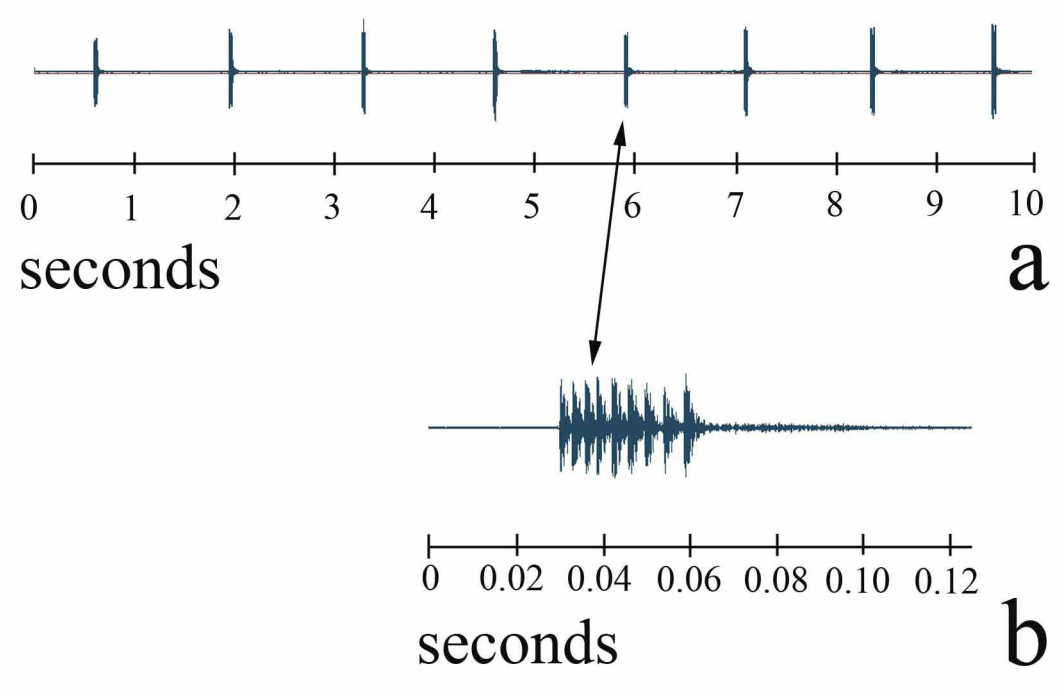

FIGURE 8. Oscillogram of *Phymonotos jacintotopos* **gen. et sp. nov.,** lab recording at 23 C. See text for explanation.

Phymonotus males may produce thoracic gland secretions (Gwynne 2001) as a nuptial meal for females prior to and during mating. D. C. F. Rentz (personal communication April, 2011) informed us that E. R. Tinkham reported to him that males produced a fluid from under the tegmina during courtship, and that females fed upon the fluid prior to mating. We did not observe courtship, mating, or thoracic gland secretions in *Phymonotus*, but we did find evidence of dried fluid on the dorsal postnotal segment and first abdominal tergite of many pinned male specimens. We did not find any evidence of visible gland openings, but the dorsal postnotal segment of *Phymonotus* males does possess shallow lateral depressions that may serve to retain fluid. Thoracic gland secretions might be extruded from membranes under the dorsal postnotal segment. Such thoracic gland secretions are known to be secreted from the metanotal gland by male tree crickets (*Oecanthus*) (Walker and Gurney 1967), and the secretions are known to increase insemination and to extend the reproductive life-span of female black-horned tree crickets (*Oecanthus nigricornis* F. Walker) (Brown 1997). We did not find evidence that females chew on the male wings, also an indication of nuptial meals offered by male hump-winged crickets (*Cyphoderris*) to females during courtship and mating (Gwynne 2001). Examination of numerous pinned specimens of *Agalothorax* and *Neduba* males revealed no indication of dried thoracic gland secretions as found in *Phymonotus*, but both genera do possess the same lateral depressions in the dorsal postnotal segment as we found in *Phymonotus*. Further research should be conducted to determine the presence and nature of thoracic gland secretions in *Phymonotus*, a feature unknown in any other Nedubini or Tettigoniini world-wide.

Distribution. *Phymonotus* is known only from the San Jacinto Mountains, Riverside County, California (Fig 3). *Phymonotus* has been found only in the Fern Valley and Boulder Basin Campground areas on the west side of the San Jacinto Mountains near the town of Idyllwild, from approximately 1,500 m to 2,500 m elevation. Despite extensive field surveys by us in the nearby San Bernardino, San Gabriel, and Tehachapi Mountains, which also

support conifer forests and related *Agalothorax* and *Neduba* species, no *Phymonotus* were heard. Other related *Agalothorax* and *Neduba* taxa occur throughout southern California at lower elevations in chaparral, pinyon/juniper woodland and desert shrub, especially on Joshua tree (*Yucca brevicauda*).

Discussion

The taxonomy and classification of North American Nedubini were reviewed by Rentz and Birchim (1968), and the Nedubini of the world by Rentz and Colless (1990). The genera *Agalothorax* and *Neduba* have been historically classified both as separate genera (Caudell 1907, Rehn and Hebard 1920) and as subgenera of *Neduba* (Rentz and Birchim 1968), but most recently (Rentz 1988, p. 232) both were formally raised to full genera. We now add the genus *Phymonotus* to those two genera to comprise the North American Nedubini.

Rentz and Colless (1990) included *Phymonotus* as an unnamed genus (coded GNT4) in their phylogenetic analysis of world Tettigoniinae based on morphological characters. They found *Phymonotus* to be a sister group to *Agalothorax* and *Neduba*, forming a North American clade of Nedubini. Cole (2009) also included *Phymonotus* as an unnamed genus (coded Jcp) in a molecular DNA phylogenetic analysis of the species of *Agalothorax*, using *Neduba* as an out-group, and also found *Phymonotus* to be a sister group to *Agalothorax* and *Neduba*.

The Nedubini have a geographic distribution consistent with Gondwanan ancestry, represented by extant taxa in Australia and South America (Rentz and Colless 1990). However, the Nedubini genera *Agalothorax*, *Neduba* and *Phymonotus* occur on the west coast of North America, not consistent with Gondwanan ancestry. Ancestral North American Nedubini apparently dispersed to western North America from South America. A unique morphological feature of North American Nedubini is a laterally expanded and flattened shield-like pronotum, especially the metazona that is distinctly more enlarged than any other Nedubini from South America or Australia or any other Tettigoniinae world-wide (Rentz and Gurney 1985, Rentz and Colless 1990). *Phymonotus* is further distinct from other Nedubini in that the enlarged pronotum is not flat and shield-like, rather the metazona is rounded and elevated like a dome, unlike any species of *Agalothorax* or *Neduba*, or any other genus of Tettigoniinae. We speculate that this dome-like metazoan, which surrounds the wings, serves as an amplifying structure for the male's calling song, especially since the feature is more pronounced in males than females. The dome-shaped metazona also may project sound in such a way as to confuse potential predators as to the male's location.

Another morphological character that is unique to the Nedubini is the highly modified and enlarged male paraprocts relative to other Tettigoniinae. Male paraprocts in most Tettigoniinae are flat elongate structures that are located at the terminus of the male abdomen, beneath the posterior edge of the supra anal plate, or ultimate posterior tergite (tergite 10), and between the cerci. The cerci of most Tettigoniinae are enlarged and modified to serve as clasping organs for mating, but in the Nedubini the cerci are reduced to simple non-clasping structures (Rentz and Colless 1990). In contrast, it is the paraprocts of the Nedubini that are enarged and modified to function as the clasping organs in mating. For this reason, the paraprocts of Nedubini are often referred to as "pseudocerci" (Rentz and Colless 1990). The female ovipositors of North American Nedubini also are unique in that they are armed with a series of teeth on both the dorsal and ventral valves near the apices (Rentz and Birchim 1968).

Agalothorax, *Neduba* and *Phymonotus* all produce calling songs that are distinctive between the three genera. Rentz and Weissman (1981) and Cole (2009, 2010) found *Agalothorax* to produce calling songs consisting of closely spaced, single pulses of a variable number (but always more than one); *Neduba* to produce continuous songs or pulse trains, consisting of more than one pulse type; and *Phymonotus* to produce only spaced, single pulses.

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APPENDIX 1. Illustrated guide to morphological measurements taken from *Phymonotus jancintotopos* specimens.

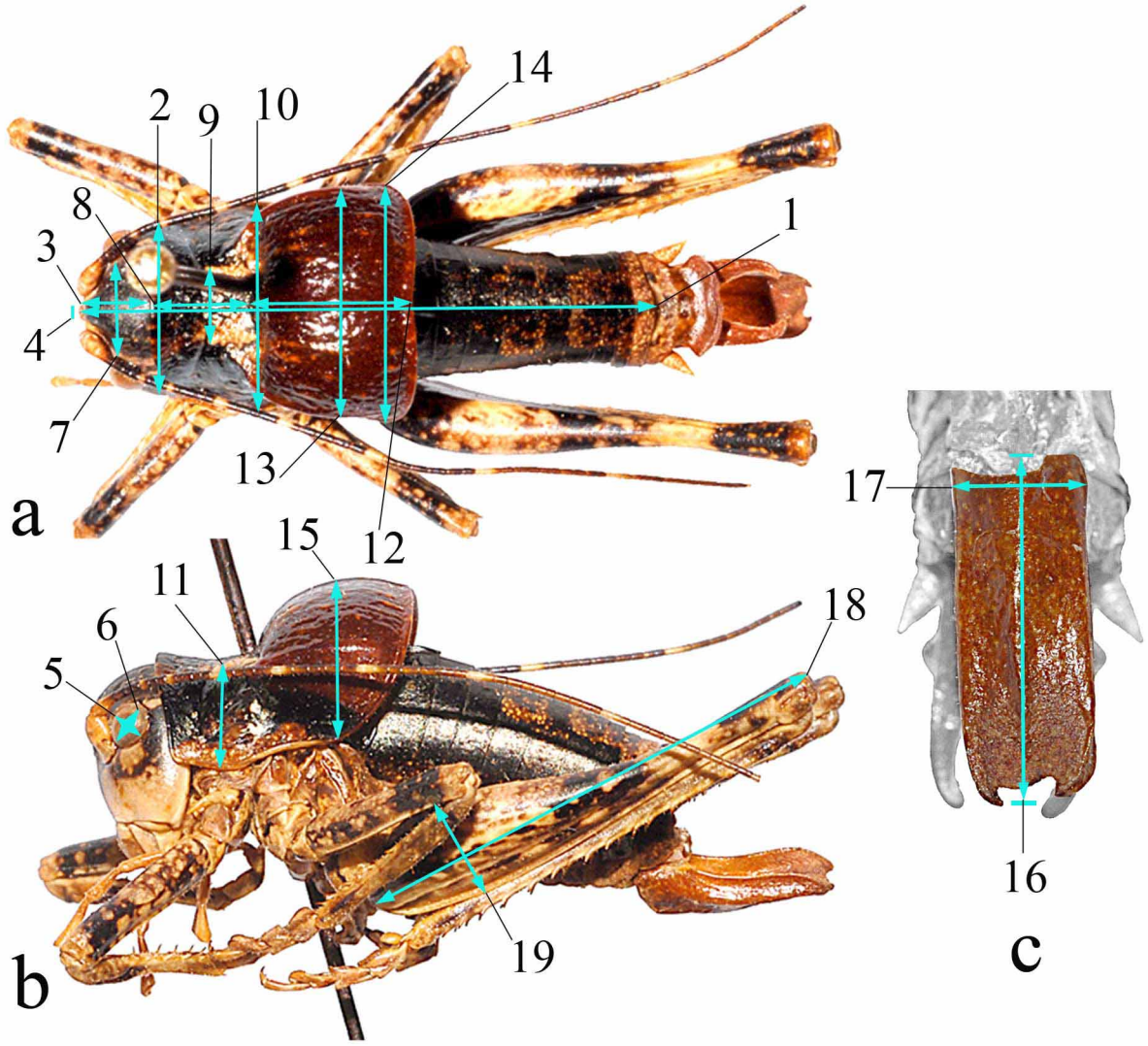
Male measurements (Appendix Fig 1.1).

1. Body Length
2. Head Width
3. Head Length
4. Head Vertex Width
5. Eye Width
6. Eye Height
7. Inter-eye Distance
8. Prozona Length
9. Prozona Dorsal Width
10. Prozona Ventral Width
11. Prozona Depth
12. Metazona Length
13. Metazona Dorsal Width
14. Metazona Ventral Width
15. Metazona Depth
16. Subgenital Plate Length
17. Subgenital Plate Width
18. Hind Femur Length
19. Hind Femur Width

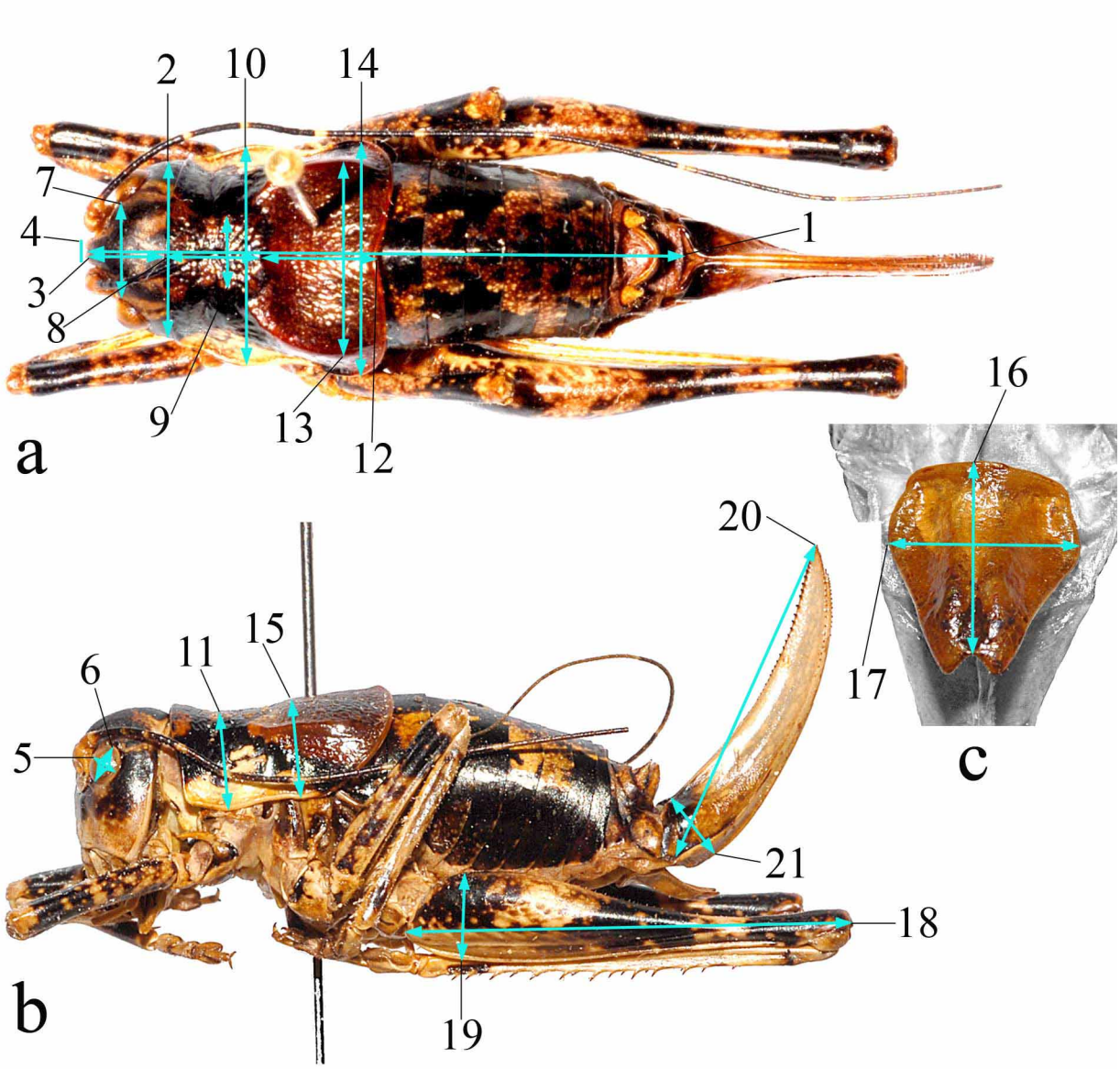
Female measurements (Appendix Fig 1.2)

1. Body Length
2. Head Width
3. Head Length
4. Head Vertex Width

5. Eye Width
6. Eye Height
7. Inter-eye Distance
8. Prozona Length
9. Prozona Dorsal Width
10. Prozona Ventral Width
11. Prozona Depth
12. Metazona Length
13. Metazona Dorsal Width
14. Metazona Ventral Width
15. Metazona Depth
16. Subgenital Plate Length
17. Subgenital Plate Width
18. Hind Femur Length
19. Hind Femur Width
20. Ovipositor Length
21. Ovipositor Width



APPENDIX 1, Fig 1.1. Morphological measurements taken from *Phymonotus jacintotopos* males. Numbers correspond to the list of male measurements; a. dorsal view; b. lateral view; c. subgenital plate, ventral view.



APPENDIX 1, Fig. 1.2. Morphological measurements taken from *Phymonotus jacintotopos* females. Numbers correspond to the list of female measurements; a. dorsal view, b. lateral view; c. subgenital plate, ventral view.