

**Figures 31–33** Comparisons of *Hadrurus obscurus* and *H. spadix*, metasomal segments II–III, ventral view, showing diagnostic setation located between the ventromedian (VM) carinae. **31.** *H. obscurus*, male (pale phenotype, segment II length = 8.44 mm, segment III length = 9.26 mm), Bird Spring Canyon Road, Kern Co., California, USA. **32.** *H. obscurus*, female (dark phenotype, segment II length = 5.02 mm, segment III length = 5.70 mm), Bird Spring Canyon Road, Kern Co., California, USA. **33.** *H. spadix*, female (segment II length = 7.87 mm, segment III length = 8.36 mm), Apex Mine in Curly Hollow Wash, Washington Co., Utah, USA.

19). However, to support our suspicion, we have examined two *H. obscurus* specimens collected from the same locality where one has a carapace pattern of *H. spadix* and the other a pattern typical of *H. obscurus* (see Fig. 20 for color closeup images of these carapaces, and Figs. 9–10 for overall comparison with “*arizonensis*” group species). Based on these data, we suggest here that these carapacial pattern differences are analogous to those exhibited by the dark and pale phenotypes of *H. anzaborrego*, and therefore, *H. obscurus* is only a color-variant phenotype of *H. spadix*. The nine specimens from Inyo County, which we have not personally examined (trichobothria data courtesy of Matthew R. Graham), intersect with the known range of *H. spadix*. Of the 18 specimens we have personally examined (five from Los Angeles County, and 13 from Kern County), only the latter locality is somewhat close to the south-central populations reported by Williams (1970). Since we have not had the opportunity to view specimens of *H. obscurus* and *H. spadix* from their type localities (San Benito Co., California and northern Arizona, respectively), we defer acting upon this suspicion until adequate material becomes available.

As stated above the positions and numbers of chelal internal trichobothria are essentially identical in *Hadrurus obscurus* and *H. spadix*, while both numbers and positions differ in *H. anzaborrego* (see Fig. 19). *H. anzaborrego* has three internal accessory trichobothria whereas the other two species have two. Statistics involving over 250 samples show that these numerical differences are observed in over 87 % of the specimens examined (Fig. 21). The MVD and *p*-value (ANOVA) between these two data sets are 39.6 % and 2.37E-52, respectively. In addition, it is clear in Fig. 19 that the relative spacing of the individual accessory trichobothria in the two patterns is different, occurring more distally and proximally on the palm in *H. anzaborrego*. UV photographs in Figs. 22–33 show in detail the trichobothrial and metasomal setal patterns of both dark and pale phenotypes of *H. obscurus* as compared to *H. spadix* from Inyo Co., California.

The carapacial patterns are distinct in *H. anzaborrego*, not matched in either of the two northern species (see Fig. 19). In addition, *H. anzaborrego* is consistent with the dark/pale phenotype scenarios we see in *H. arizonensis arizonensis*, which, as suggested above

for *H. spadix* and *H. obscurus*, again supports its distinctness. See Figs. 57–58 for photos of live specimens of these two color-based phenotypes.

### Molecular observations

Fet, Soleglad & Barker (2001) conducted the first molecular-based analysis of the genus *Hadrurus*. Germane to this study is their analysis specific to the “*arizonensis*” group, which we briefly highlight here. Mitochondrial DNA markers (a portion of 16S mtDNA gene) were amplified and compared from 19 *Hadrurus* specimens, including 16 specimens from the “*arizonensis*” group of *Hadrurus*, eleven *H. arizonensis* (both dark and pale phenotypes), one *H. spadix*, and four *H. anzaborrego* (referred to as *H. obscurus*), two each of the dark and pale phenotypes. In addition to morphology-based analysis, molecular algorithms exercised included genetic distance, parsimony, maximum likelihood using five gene substitution models, cluster analysis (UPGMA and NJ), and direct optimization (POY). In particular, the absolute genetic distance exhibited between the “*arizonensis*” and “*spadix*” subgroups as well as species within the “*spadix*” subgroup are applicable to this contribution (see Fet, Soleglad & Barker, 2001: tabs. 1, 3).

The uncorrected absolute distance shown between the eleven “*arizonensis*” and five “*spadix*” subgroup specimens ranged from 5.7 to 8.1 % (i.e., 21–29 base pair mismatches out of 369 bases). The percentage of mismatches within the eleven “*arizonensis*” subgroup specimens is also interesting, 0.0 to 2.3 % (i.e., 0–8 base-pair mismatches). However, out of these eleven specimens, which includes six dark and five pale phenotypes, two dark phenotypes from Arizona exhibited zero mismatches with two pale phenotypes from Borrego Springs, California. This provided the primary reason for synonymizing subspecies *H. arizonensis pallidus* (i.e., subspecies name assigned to the pale phenotype) by Fet, Soleglad & Barker (2001). Within the “*spadix*” subgroup, the single *H. spadix* sequence (a specimen from Hawthorne, Nevada) exhibited a 2.2 to 2.7 % difference (i.e., 8–10 base pair mismatches) from the four *H. anzaborrego* sequences. Of particular importance to this paper, we see that four *H. anzaborrego* sequences, based on two dark and pale phenotypes each, showed only 0 to 0.8 % difference (i.e., 0–3 base pair mismatches). These sequences were from specimens collected in Culp Valley Camp and Borrego Springs (dark phenotypes), and Pinyon Mountain and Indian Gorge Canyon (pale phenotypes). As can be seen in the map in Fig. 56, these four sequences are from specimens from various areas in the ABDSP, representing different habitats and plant communities, and different elevations (764 to 3577' asl). In particular, the sequences from Borrego Springs and

Pinyon Mountain exhibited zero differences, thus providing an example of zero difference between a dark and pale phenotype. The highest genetic difference observed in the four *H. anzaborrego* sequences was between the dark phenotype from Culp Valley Camp and the pale form from Indian Gorge. Incidentally, these two specimens are also found the farthest from each other geographically of the four specimens processed, roughly 28 miles.

### *Hadrurus anzaborrego* Soleglad, Fet et Lowe, sp. nov.

Figures 34–55, 57–58; Table 2

*Hadrurus arizonensis arizonensis*: Williams, 1970: 24 (in part).

*Hadrurus arizonensis arizonensis* x *H. a. pallidus* intergrades: Williams, 1970: 26 (in part).

*Hadrurus obscurus*: Soleglad, 1976: 114; Williams, 1980: 24, fig. 23; Fet, Soleglad & Barker, 2001: 141; Soleglad & Fet, 2003: 8; Fet et al., 2004: 18; Prendini & Wheeler 2005: 454; Fet et al., 2006: 269; Fet, Soleglad & Brewer, 2006: 3; Fet & Soleglad, 2008: 257; Soleglad & Fet, 2010: 2.

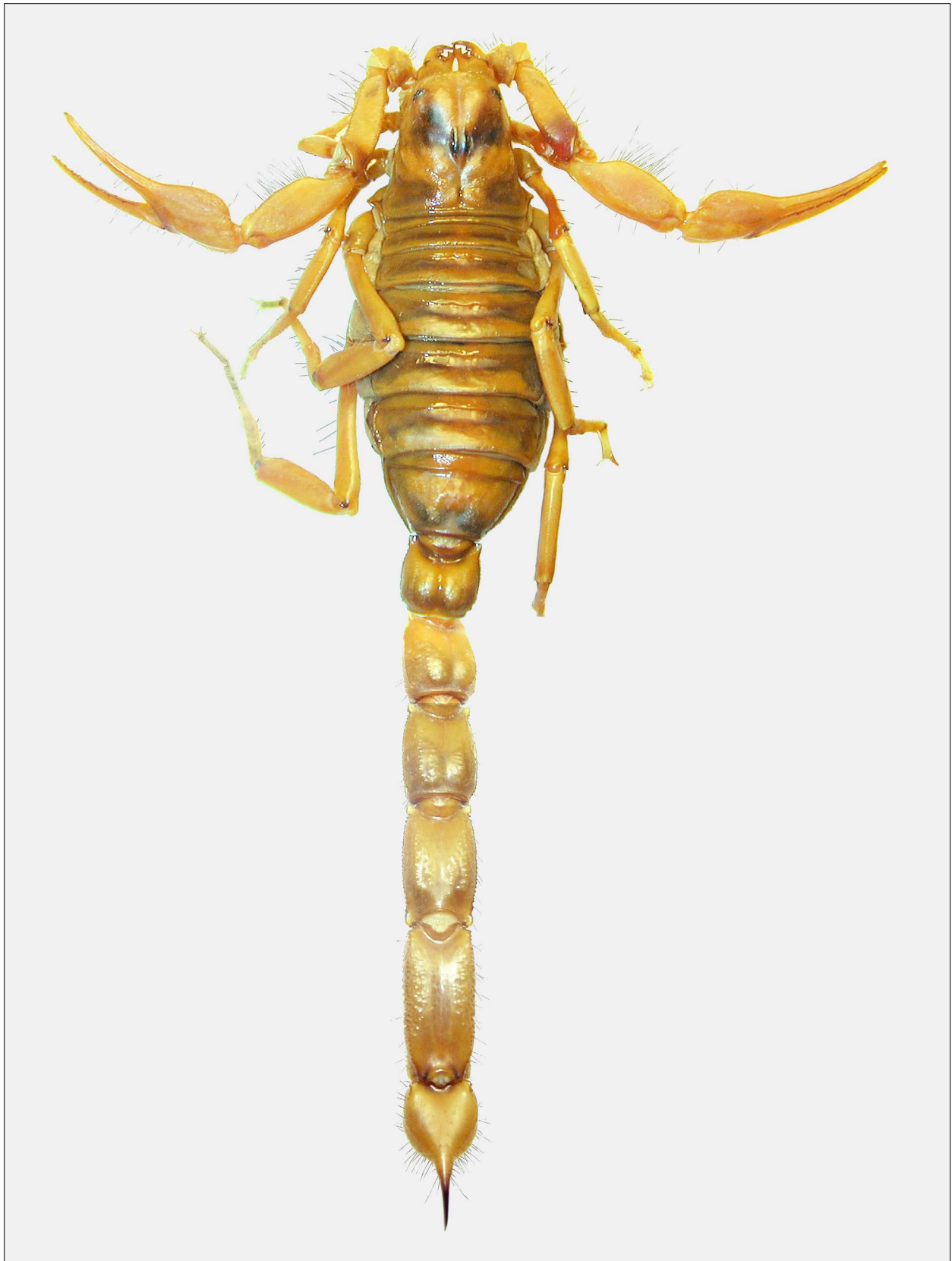
*Hadrurus obscurus* (in part): Kovařík, 1998: 136; Sissom & Fet, 2000: 417; Francke & Prendini, 2008: 206, 220.

**Holotype:** female, Indian Gorge Canyon, 1.7 mi. W of S-2, ABDSP (32.874, -116.235; 1083'), San Diego County, California, USA, 22 June 1998 (M. E. Soleglad) (MES).

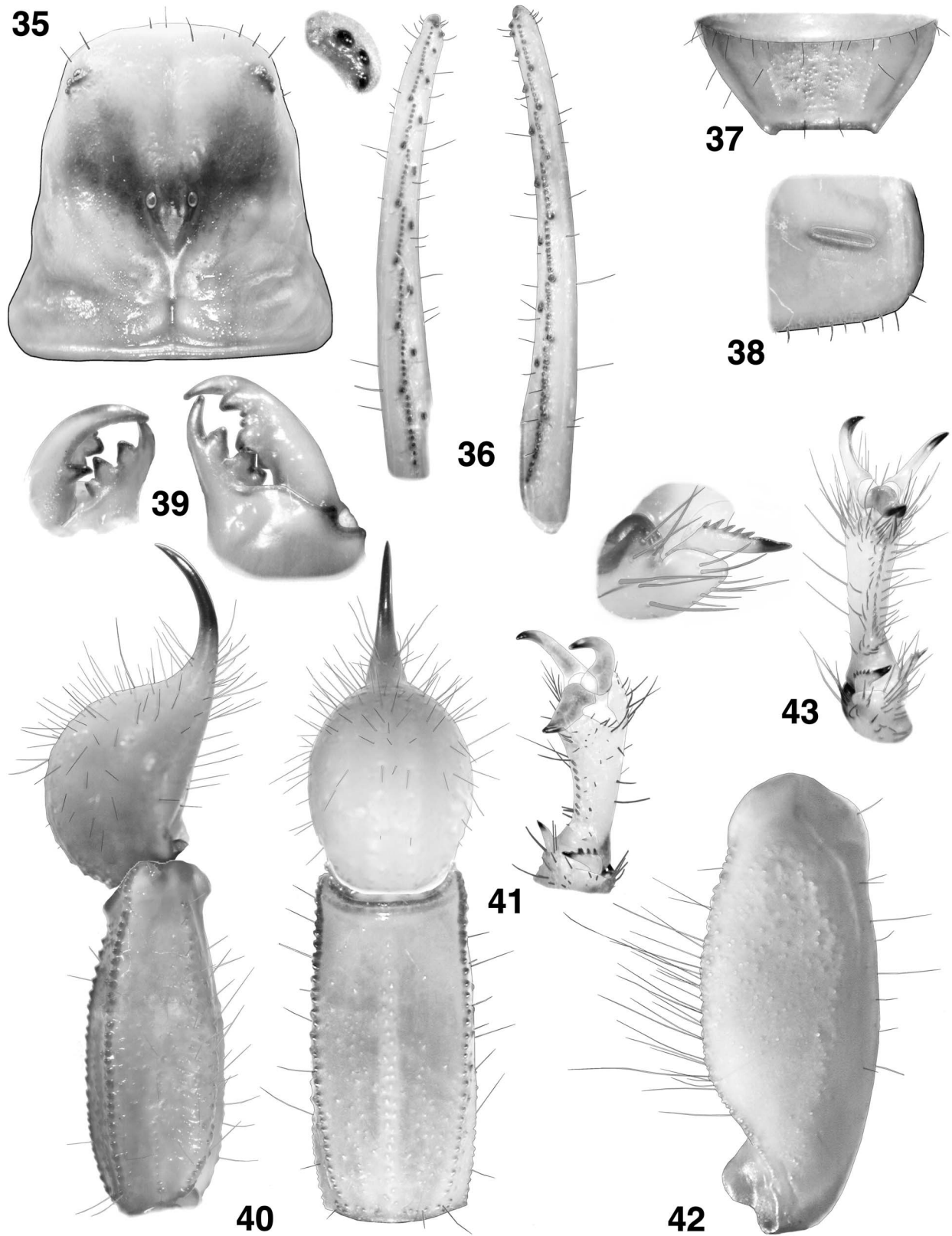
**Diagnosis:** Medium sized (100–110 mm) member of “*spadix*” subgroup. Chelal external accessory trichobothria absent, 2–4 (3.0) internal accessory trichobothria, 13–17 (15.0) ventral trichobothria. Carapace interocular area with distinct V-shaped clear pattern extending from lateral eyes to the median eyes, posterior portion of carapace and mesosoma variable, either melanic or clear; chelal fingers lightly pigmented in contrast to palm. Setation found between ventromedian (*VM*) carinae of metasomal segments I–III. Telson aculear glands on mature males absent. Pectinal teeth, 35–41 (38.32) in the male and 28–34 (30.40) in the female.

**Distribution:** USA; Mexico. Restricted to the Colorado Desert region, as far north as southern Joshua Tree National Monument, throughout the ABDSP, and south into extreme northern Baja California.

**Etymology:** Named after the Anza-Borrego Desert State Park in southern California, USA, from where the species was originally collected.



**Figure 34:** *Hadrurus anzaborrego*, sp. nov. Female holotype, Indian Gorge Canyon, ABDSP, California, USA. Dorsal view.



**Figures 35–43:** *Hadrurus anzaborrego*, sp. nov.. 35–42. Female holotype, Indian Gorge Canyon, ABDSP, California, USA. 43. Male paratype, Yaqui Pass Road, ABDSP, California, USA. 35. Carapace and close-up of lateral eyes. 36. Chelal fixed and movable finger dentition. 37. Sternite VII. 38. Stigma, left II. 39. Chelicera, ventral and dorsal views. 40. Metasomal segment V and telson, lateral and ventral views. 41. Right leg II, tarsus, ventral view. 42. Pedipalp patella, dorsal view. 43. Left leg IV, tarsus, ventral view. Note spinelets on internal pedal spur shown in closeup.

<i>Hadrurus anzaborrego</i> , sp. nov.				
	Indian Gorge Canyon, ABDSP, California, USA	Palm Canyon Trail, ABDSP, California, USA	Yaqui Pass Road, ABDSP, California, USA	Culp Valley Area, ABDSP, California, USA
	Female Holotype	Female Paratype	Male Paratype	Male Paratype
Total length	104.30	107.90	99.35	84.90
Carapace length	13.20	13.55	11.65	11.45
Mesosoma length	29.95	33.85	26.25	21.60
Metasoma length	47.20	46.55	48.75	40.00
Segment I length/width	6.60/7.10	6.35/6.75	7.40/5.70	5.95/5.95
Segment II length/width	7.60/6.85	7.60/6.35	8.25/5.50	7.00/5.70
Segment III length/width	8.90/6.60	8.90/6.35	9.10/5.50	7.60/5.50
Segment IV length/width	10.65/6.60	10.60/6.15	10.60/5.70	8.45/5.50
Segment V length/width	13.45/6.35	13.10/5.95	13.40/5.50	11.00/5.50
Telson length	13.95	13.95	12.70	11.85
Vesicle length	10.15	9.30	7.60	8.05
width/depth	6.10/5.85	6.35/5.50	5.10/4.65	5.30/5.10
Aculeus length	3.80	4.65	5.10	3.80
Pedipalp length	41.65	41.90	38.50	35.75
Femur length/width	10.65/3.05	10.60/2.95	10.15/2.95	9.10/2.95
Patella length/width	11.70/4.55	11.85/4.25	11.00/4.25	10.15/3.80
Chela length	19.30	19.45	17.35	16.50
Palm length	7.10	7.00	6.75	5.50
width/depth	4.05/6.10	4.25/6.15	3.60/5.50	3.40/4.65
Fixed finger length	10.90	11.00	10.15	9.30
Movable finger length	13.20	13.55	13.10	11.85
Pectines teeth	30-31	30-31	35-36	41-39
middle lamellae	17-19	20-18	18-15	23-21
Sternum length/width	2.25/2.90	2.10/2.70	1.95/2.05	1.70/2.15

**Table 2:** Morphometrics (mm) of *Hadrurus anzaborrego*, sp. nov.

**FEMALE.** Description based on holotype female except where noted. See Fig. 34 for dorsal view of female holotype and Table 2 for measurements.

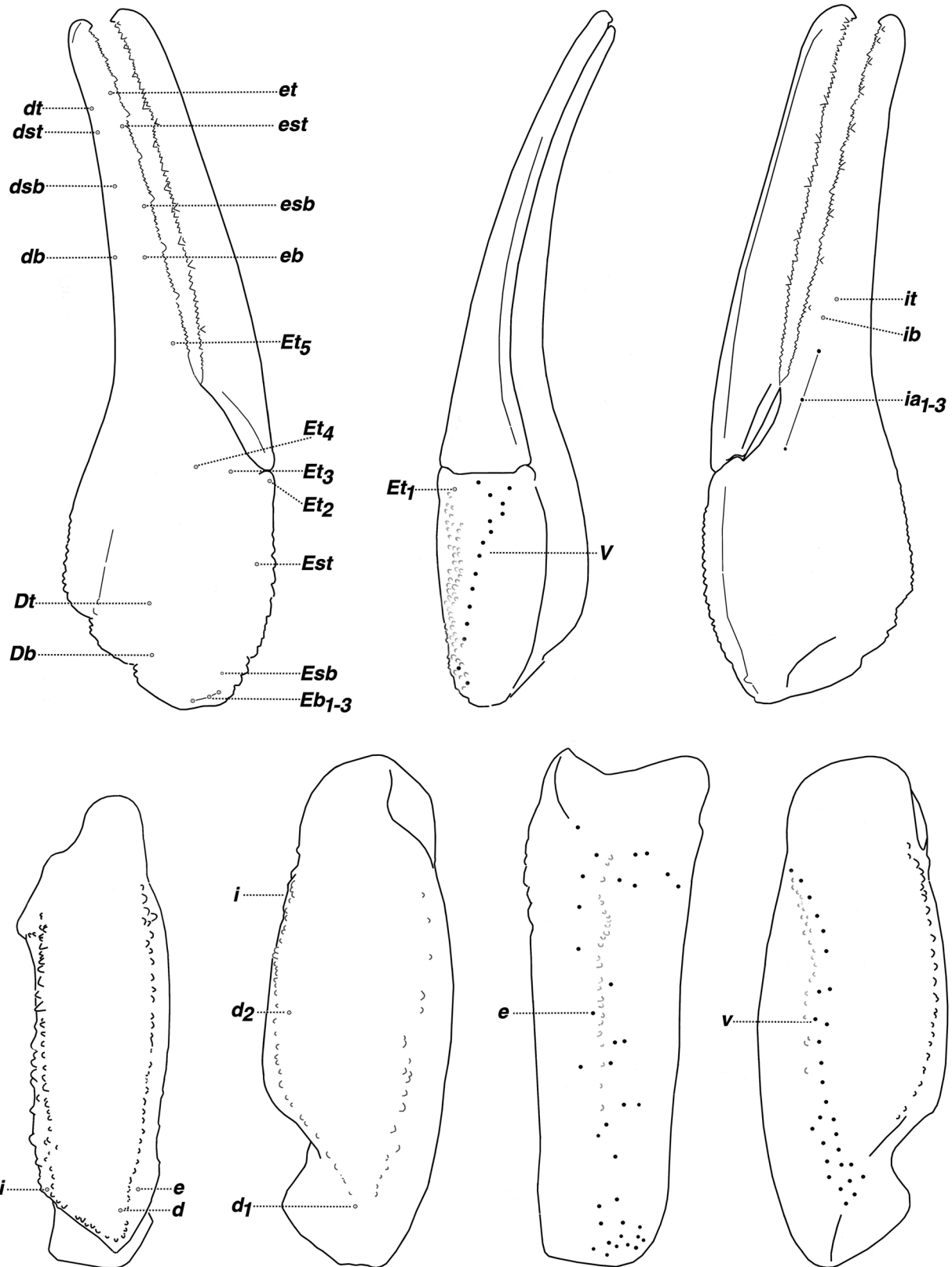
**COLORATION.** Background color of mesosoma, metasoma, telson, pedipalps, and legs pale yellow. Carapace interocular area with distinct V-shape melanic pattern in contrast to pale yellow background. Sternites, pectines, basal piece, genital operculum medium brown. Leg condyles, cheliceral fingers, aculeus dark brown. Chela fingers originally reddish, but faded due to preservation.

**CARAPACE (Fig. 35).** Anterior edge convex with nine scattered irregularly sized setae; anterior edge length as compared to median eye tubercle position in ratio of 0.253. Wide shallow median indentation extending from median tubercle to anterior edge. Interocular area essentially smooth, small granules scattered on lateral and caudal edges. Lateral eyes three in number, the most proximal the smallest. The median eyes, positioned

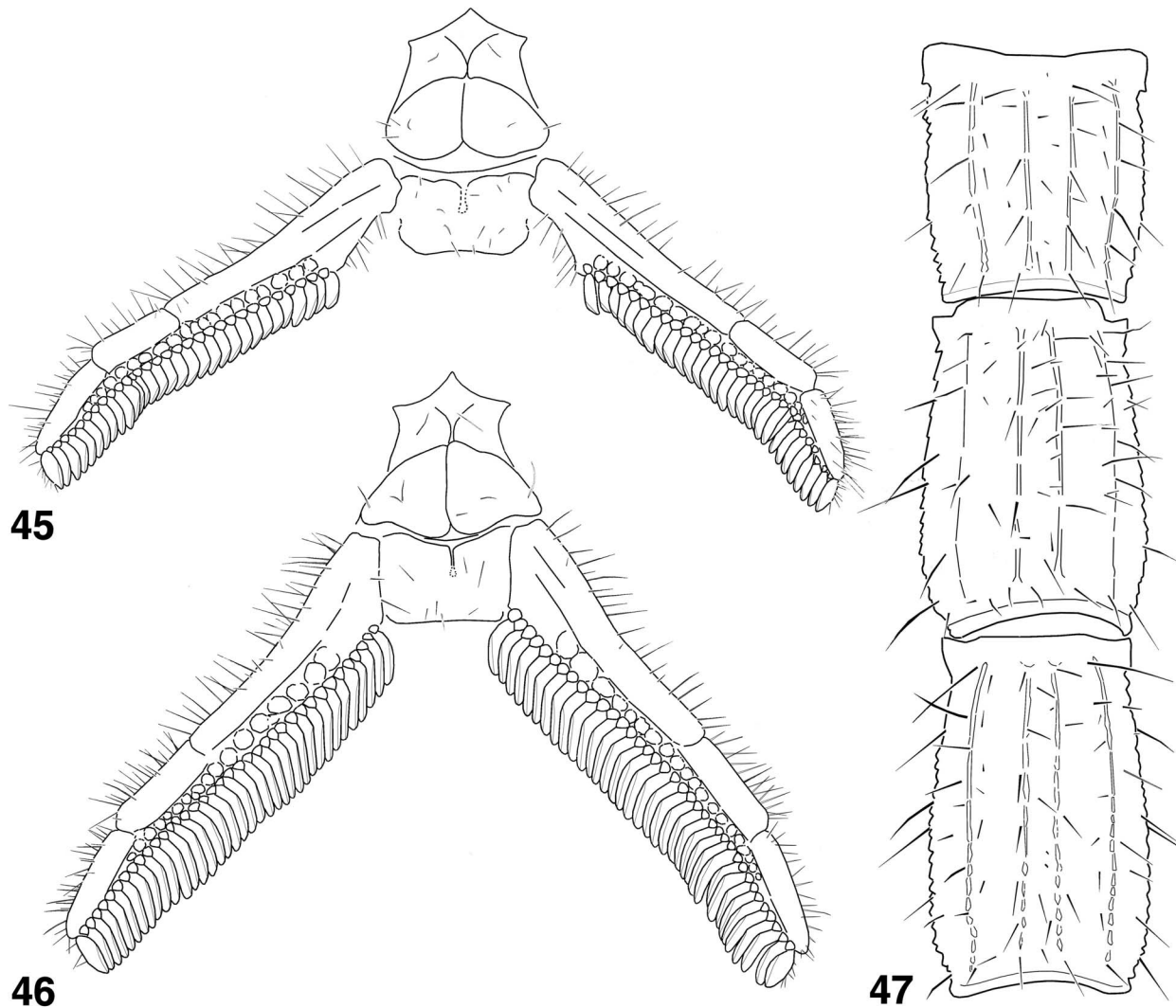
wide-set on a smooth tubercle, are positioned slightly proximal of midpoint with the following length and width ratios: 0.527 (anterior edge to median tubercle middle / carapace length) and 0.200 (width of median tubercle including eyes / width of carapace at that point).

**MESOSOMA (Figs. 37–38).** Tergites I–VI are basically smooth except for minute granulation on extreme posterolateral edges. Tergite VII lateral areas largely covered with scattered large granules, showing slight traces of lateral and median carinae. Sternites III–VI smooth and lustrous; sternite VII lateral carinae crenulate, median carinae present but obscured by scattered granules. Stigmata elongated, slit-like in shape, angled 12° in an anterointernal direction.

**METASOMA (Fig. 40).** Segment I is wider than long. Segments I–IV: dorsal carinae granulated on I–II and crenulated on III–IV; dorsolateral carinae granulated on I and crenulated on II–IV; lateral carinae granulated on



**Figure 44:** *Hadrurus anzaborrego*, sp. nov. Female holotype, Indian Gorge Canyon, ABDSP, California, USA. Trichobothrial pattern showing neobothriotaxy. Accessory trichobothria are indicated by closed circles. Note that chelal ventral and patellar ventral and external orthobothriotaxic trichobothria are not distinguished from accessory trichobothria.



**Figures 45–47:** *Hadrurus anzaborrego*, sp. nov.. **45.** Sternopectinal area, female holotype, Indian Gorge Canyon, ABDSP, California, USA. **46–47.** Male paratype, Yaqui Pass Road, ABDSP, California, USA. **46.** Sternopectinal area. **47.** Metasomal segments I–III, diagrammatic ventral view, showing diagnostic setation located between the ventromedian (VM) carinae. Note, the minute setae on the pectinal fulcra and middle lamellae are not shown.

I, posterior three-fifths of II and III, and posterior half on IV; ventrolateral carinae smooth to granulated on I–III and crenulated on IV; ventromedian carinae smooth to granulated on I, smooth on II, smooth to granulated on III, and crenulated on IV. Dorsolateral terminus slightly flared, not meeting condyle. Segment V: Dorsolateral carinae rounded and granulated; lateral carinae irregularly granulated on anterior two-fifths; ventrolateral carinae crenulated to serrated, and single ventromedian carina irregularly crenulated with a straight terminus. Anal arch with approximately 25 small rounded pigmented granules. Dorsal surface of segments IV–V covered with long setae; ventromedian intercarinal area with 6-5-6 setae on segments I–III.

**TELSON (Fig. 40).** Large globular vesicle with long highly curved aculeus, subaculear tubercle and aculear

glands absent. Ventral and lateral surface of vesicle covered with moderately large granules. Distal two-thirds of vesicle and base of aculeus covered with numerous elongated setae. Vesicular tabs with 2–4 rounded granules.

**PECTINES (Fig. 45, male paratype Fig. 46).** Large well developed elongated structures, exhibiting length / width ratio 4.762 (length taken at anterior lamellae / width at widest point including teeth). Three anterior lamellae are present, the most proximal considerably elongated, three times longer than second lamella, which is slightly shorter than the distal lamella. 17/19 bead-like middle lamellae and well developed fulcra are present. Sensorial areas present on all teeth, which number 30–31. Numerous elongated setae emanate anteriorly from the anterior lamellae; distal pectinal tooth covered laterally

with setae; and each fulcrum and middle lamella found with two to three minute setae. Basal piece large, with deep median indentation on anterior edge (2/5 of segment length); length / width ratio 0.563.

**GENITAL OPERCULUM (Fig. 45).** Large sclerites completely separated for most of length, with inner posterior edges highly rounded.

**STERNUM (Fig. 45).** Type 2, posterior emargination present, well-defined convex lateral lobes, apex visible and very deep-set and conspicuous; sclerite wider than long, length / width ratio 0.776; sclerite tapers anteriorly, posterior-width / anterior-width ratio 1.151 (see discussion on male below).

**CHELICERAE (Fig. 39).** Movable finger dorsal edge with two small subdistal (*sd*) denticles; ventral edge with one large pigmented accessory denticle located on basal 1/3 of finger; ventral edge serrula absent. Ventral distal denticle (*vd*) longer than dorsal (*dd*). Fixed finger with four denticles, median (*m*) and basal (*b*) denticles conjoined on common trunk; no ventral accessory denticles are present.

**PEDIPALPS (Figs. 36, 42, 44).** Medium size appendages, lightly carinated chelae with elongated fingers. Chelal fingers not scalloped or exhibiting finger lobes. Patella internal surface covered with numerous elongated straight setae (Fig. 42). Femur: Dorsointernal, ventrointernal, and dorsoexternal carinae crenulated, ventroexternal irregularly granulated on basal one-half. Dorsal and ventral surfaces smooth, internal surface with scattered granules, and external with few low profile granules. Patella: Dorsointernal and ventrointernal carinae crenulated, dorsoexternal and ventroexternal carinae rounded and granulated, and exteromedian smooth to rough to irregularly granulated. Dorsal surface with scattered minute granules, ventral and external surfaces smooth, internal smooth lacking dorsal and ventral patellar spurs, covered with approximately 35 elongated setae. Internal basal area slightly raised in ratio of 9.67 with width between dorsal carinae. Chela carinae: Complies with the “10-carinae configuration”. Digital (*D1*) carina essentially obsolete; sub-digital (*D2*) carina marginal with two basal granules; dorsosecondary (*D3*) and dorsomarginal (*D4*) carinae rounded irregularly granulated; dorsointernal (*D5*) carina rounded and smooth; ventroexternal (*V1*) carina rounded, heavily granulated extending to external condyle; ventromedian (*V2*) carina rounded and granulated; ventrointernal (*V3*) carina rounded and smooth; external (*E*) carina obsolete. Chelal finger dentition (Fig. 36): Median denticle (MD) row groups oblique but not imbricated, numbering 9/9; 8/9 IDs on fixed finger and 9/9 IDs on movable finger; 7/8 ODs on fixed finger and 9/9 ODs on movable finger.

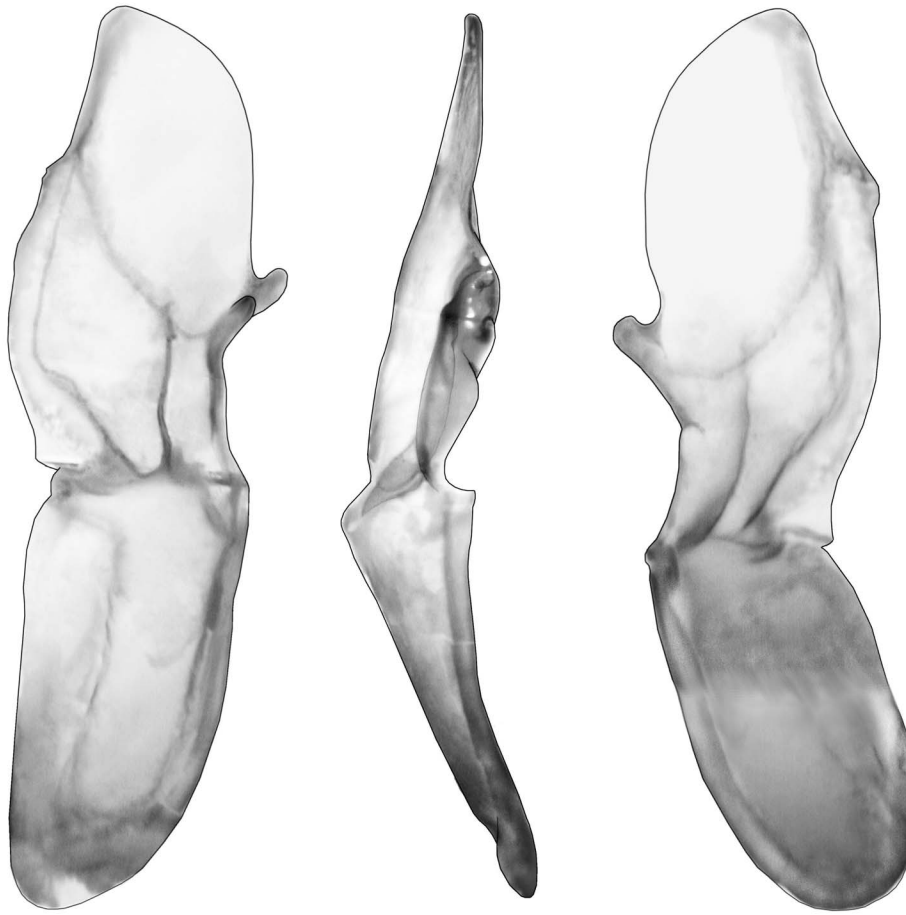
No accessory denticles present. **Trichobothrial patterns** (Fig. 44): Type C, neobothriotaxic, chela internally with 5/5 (three accessory) trichobothria, and ventrally with 16/16 (12 accessory) trichobothria; patella ventrally with 29/29 (26 accessory) trichobothria, and externally with 36/36 (23 accessory) trichobothria. Constellation array contains four sensilla (constellation array was not observed on holotype, see SEM micrograph in Fig. 50 from another specimen).

**LEGS (Fig. 41, male paratype Fig. 43).** Both pedal spurs present, each armed with pigmented spinelets; tibial spurs absent; unguicular spur pigmented, well developed, and pointed. Tarsus distal aspect covered with elongated setae, ventral surface with median row of fused spinule clusters flanked by rows of setae (fused spinules, recognition of which requires a SEM micrograph, were not observed on the holotype, see SEM micrographs in Figs. 51–53 from three other specimens). Basitarsus external edge of legs I–III with elongated, roughly parallel setae, forming a “setal comb”, with approximately 17–20 setae on legs II–III, and 12 on leg I. Leg IV basitarsus with approximately eight irregularly sized and positioned setae, not forming a comb. Basitarsus internal edge armed with irregularly sized and positioned setae on all four legs. Fused spinule cluster rows found on basitarsus as follows: leg I with densely populated ventral and external rows, leg II with densely populated ventral and moderately populated external rows, legs III–IV with moderately populated external row (see SEM micrographs in Figs. 54–55 from a male paratype specimen).

**HEMISPORMATOPHORE (Figs. 48–49).** This description is based on a male paratype specimen (pale phenotype) collected from the Pinyon Mountain area of the ABDSP. Both hemispermatophores were observed still attached to the specimen (the tergites were removed to expose the structures). From a dorsal perspective, the foot of the trunk is adjacent to the posterior edge of the carapace, the terminus of the lamina extending posteriorly beyond sternite II overlapping the anterior third of sternite III. Although the internal edges of the two hemispermatophores angle slightly towards the dorsal plane, the structures are situated essentially flat to this plane.

The right hemispermatophore is 10.6 mm in length. The hemispermatophore is a somewhat stocky structure, the wide blunted lamina slightly longer than the trunk, in a ratio 1.105. When viewing the hemispermatophore from either the internal or external edges, the median area angles outward in a dorsal direction, the lamina terminus and trunk foot pointing in a ventral direction, thus forming an obtuse angle roughly 140° (with the median area as the apex). A weak truncal flexure is visible on the external edge. The lamina is reinforced with two vertical sclerotized bolsters originating from its





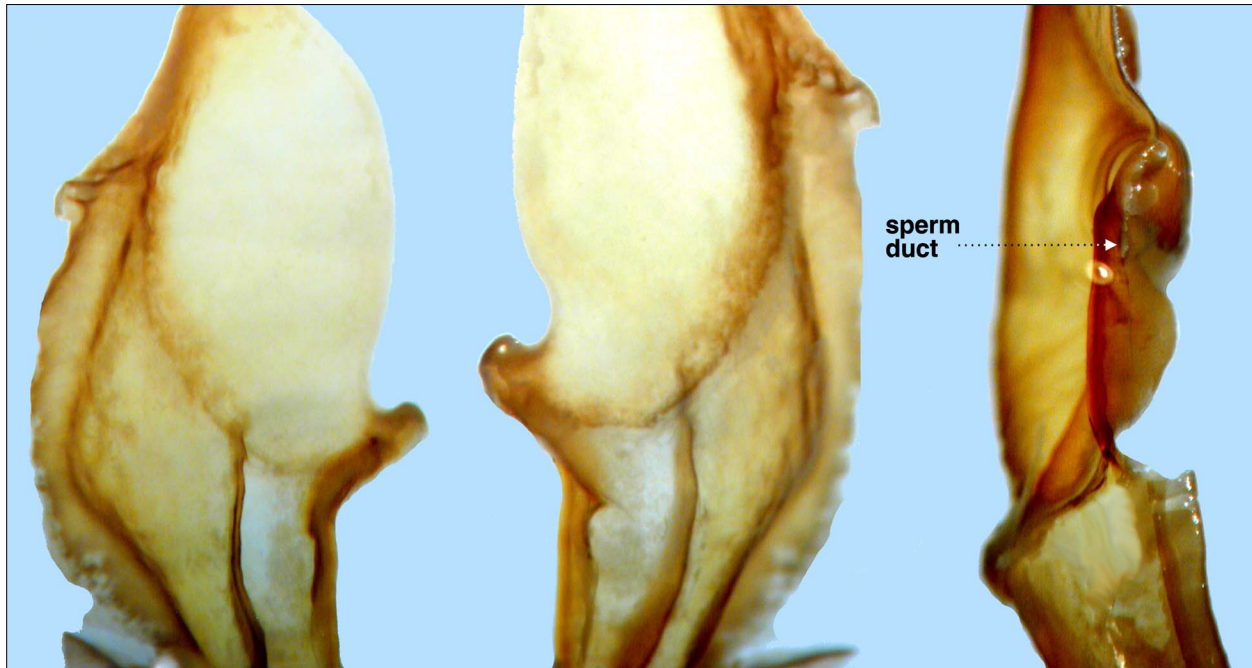
**Figure 48:** Right hemispermatophore, dorsal, internal, and ventral views, *Hadrurus anzaborrego*, **sp. nov.** (paratype male, light phenotype), Pinyon Mountain, ABDSP, California, USA.

base, one along the external edge extending distally two-thirds the lamina length, and the other positioned close to the internal edge extending roughly one-third of the lamina length. A blunt acuminate process is present on the internal edge, extending almost to the lamina midpoint in a ratio 0.444. This process is slightly bifurcated with a second subtle low-profile sclerotized dorsal terminus located just proximal of the primary process. The sperm duct is presumably located distally between these two processes (after Stockwell, 1989: fig. 215).

Note: Francke & Soleglad (1981: fig. 23–26) illustrated the hemispermatophore of *H. arizonensis* showing the *absence* of the truncal flexure. Stockwell (1989: 129, fig. 215) took exception to this stating that a weak truncal flexure was indeed present, which he illustrated for *Hoffmannihadrurus aztecus* (assigned to *Hadrurus* at that time). Based on the truncal flexure presence in *Hadrurus anzaborrego* as reported and illustrated in this paper, we suspect that it is present in all *Hadrurus* species (Soleglad et al., in progress). The hemispermatophore illustrated by Francke & Soleglad (1981) probably was not completely cleansed and therefore soft tissue may have covered the truncal flexure.

**Variability, male and female.** Pectinal teeth are longer in the male, occurring closer to the first lamella base than in the female (see Figs. 45–46). Pectinal tooth statistics for the male are 35–41 (38.318) ( $\pm 1.836$ ) [22] and the female 28–34 (30.400) ( $\pm 1.465$ ) [20], exhibiting no overlap in range and a MVD of 26 %, roughly an eight tooth difference. Separation of genital operculum at proximal edge slightly more rounded in the female. Genital papillae are lacking in the male. Intercarinal setation of *VM* carina of metasomal segments I–III is quite variable (based on 23 specimens): segment I = 0–12 (5.652) ( $\pm 3.171$ ), II = 5–19 (10.652) ( $\pm 3.663$ ), III = 3–13 (6.826) ( $\pm 2.708$ ). Pale coloration phenotype variant found in two populations, the Pinyon Mountain and Indian Gorge Canyon of the ABDSP (see Figs. 57–58 of live specimens).

**Comparative morphometrics (Tab. 2). Female holotype:** The carapace is as long as the chelal movable finger, slightly shorter than metasomal segment V (0.981) and the telson (0.946). The telson is longer than metasomal segment V (1.037). Metasomal segment I is wider than long (1.076), the other segments longer than wide (0.901–0.472). The telson vesicle is wider than deep (1.043) and as wide as the chela is deep. The chelal



**Figure 49:** Close-up of median area of right hemispermatophore submerged in alcohol, dorsal, ventral, and internal (further magnified) views. *Sperm duct* indicated (after Stockwell, 1989: fig. 215). *Hadrurus anzaborrego*, **sp. nov.** (paratype male, light phenotype), Pinyon Mountain, ABDSP, California, USA.

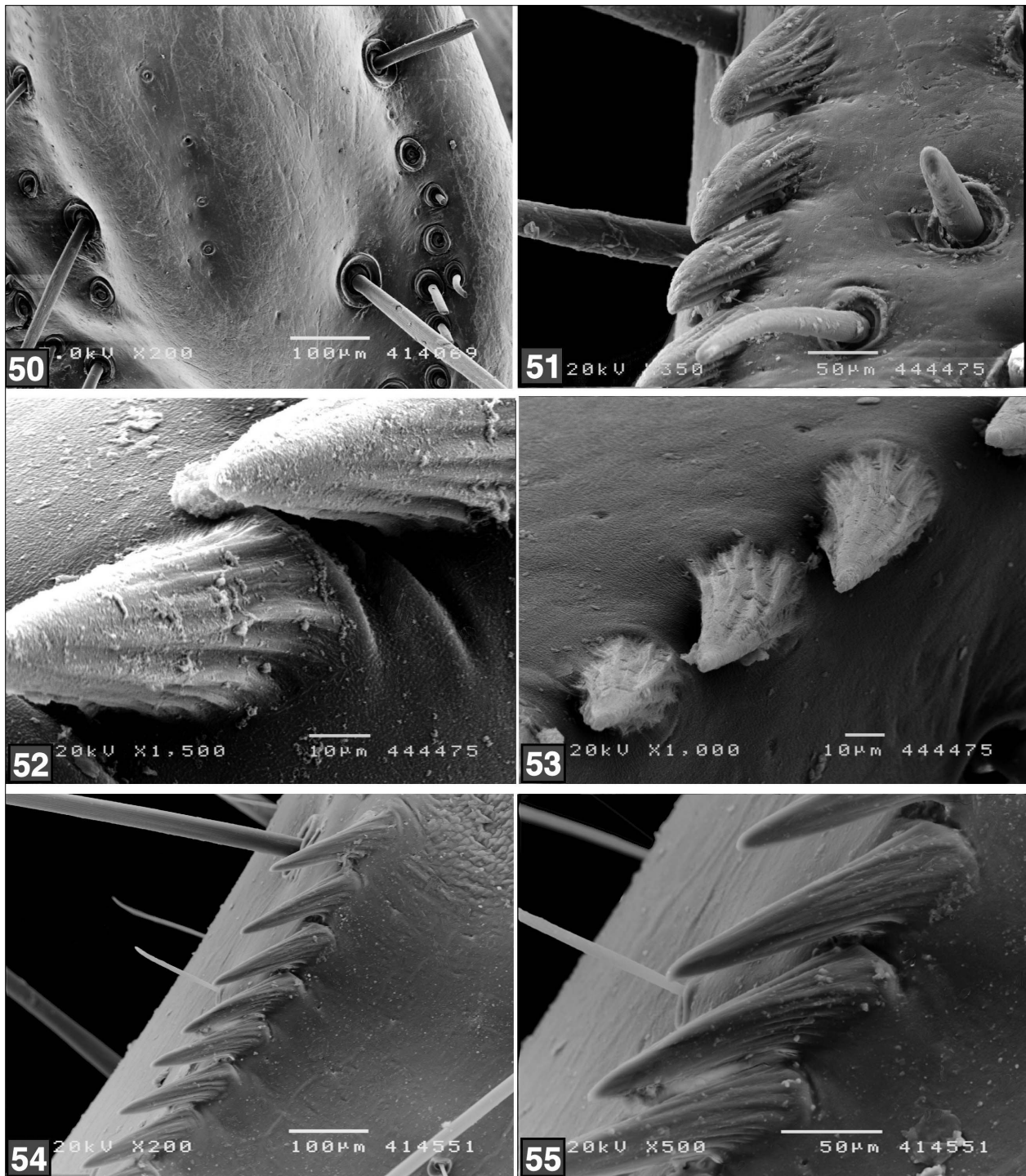
palm is deeper than wide (1.506). The sternum is wider than long (0.776). Male paratype: The carapace is shorter than the chelal movable finger (0.889), considerably shorter than metasomal segment V (0.869) and the telson (0.917). The telson is shorter than metasomal segment V (0.948). Metasomal segment I is longer than wide (0.770), the other segments longer than wide (0.667–0.410). The telson vesicle is wider than deep (1.097) and not as wide as the chela is deep (0.927). The chelal palm is deeper than wide (1.528). The sternum is wider than long (0.951).

**Dominant morphometrics, female/male (Tab. 2).** Comparing 276 possible ratios from 24 separate morphometrics between the female and male, the following five morphometrics dominated for each gender: female holotype: telson vesicle length 24/0, telson depth 23/1, metasomal segment I width, 22/2, metasomal segment II width, 21/3, and telson width 19/5. paratype male: metasomal segment I length 24/0, metasomal segment II length 23/1, metasomal segment III length 22/2, metasomal segment V length 21/3, and metasomal segment IV length 20/4. These data imply that the male has a longer, thinner metasoma whereas the female has a wider, thicker metasoma and heavier telson vesicle. Maximizing on these data (i.e., using the most dominant morphometric per gender), the morphometric ratio metasomal segment I length / vesicle length provides us with a MVD of 49.7 % between these two specimens.

**Type material. Holotype:** Adult female from Indian Gorge Canyon, 1.7 mi. W of S-2, ABDSP, San Diego County, California, USA (32.874, -116.235; 1083'), 22 June 1998 (M. Sologlad) (MES). **Paratypes** (19 specimens, all from ABDSP, San Diego County, California, USA): 1 subadult ♀, same data as in holotype; 1 adult ♂, 1 subadult ♀, Pinyon Mountain Road, 4.3 mi E of HWY-S2 (33.054, -116.353; 3577'), 20 July 1999 (M. Sologlad) (MES); 2 ♂, 1 ♀, Yaqui Pass Road, 3 mi. N of HWY-78, ABDSP, California, USA (33.159, -116.342; 1466'), 17 July 1996 (M. Sologlad) (MES); 1 subadult ♂, 1 adult ♀, 1 juvenile ♀, Palm Canyon Hiking Trail, primary trail (33.272, -116.425; 1036'), 16 April 1997 (M. Sologlad) (MES); 3 subadult ♂, 1 adult ♀, 2 subadult ♀, 1 juvenile ♀, Culp Valley Camp (33.224, -116.460; 3412'), 23 July 1996 (M. Sologlad) (MES); 1 adult ♂, Montezuma Grade, in Culp Valley area, 2.1 mi. E of Culp Valley Camp (33.211, -116.431; 2644'), 5 September 1996 (M. Sologlad) (MES); 1 subadult ♂, 1 subadult ♀, Hellhole Hiking Trail, 1–2 mi. W of Montezuma Grade (33.241, -116.408; 1279'), 29 July 1996 (M. Sologlad) (MES).

## Discussion

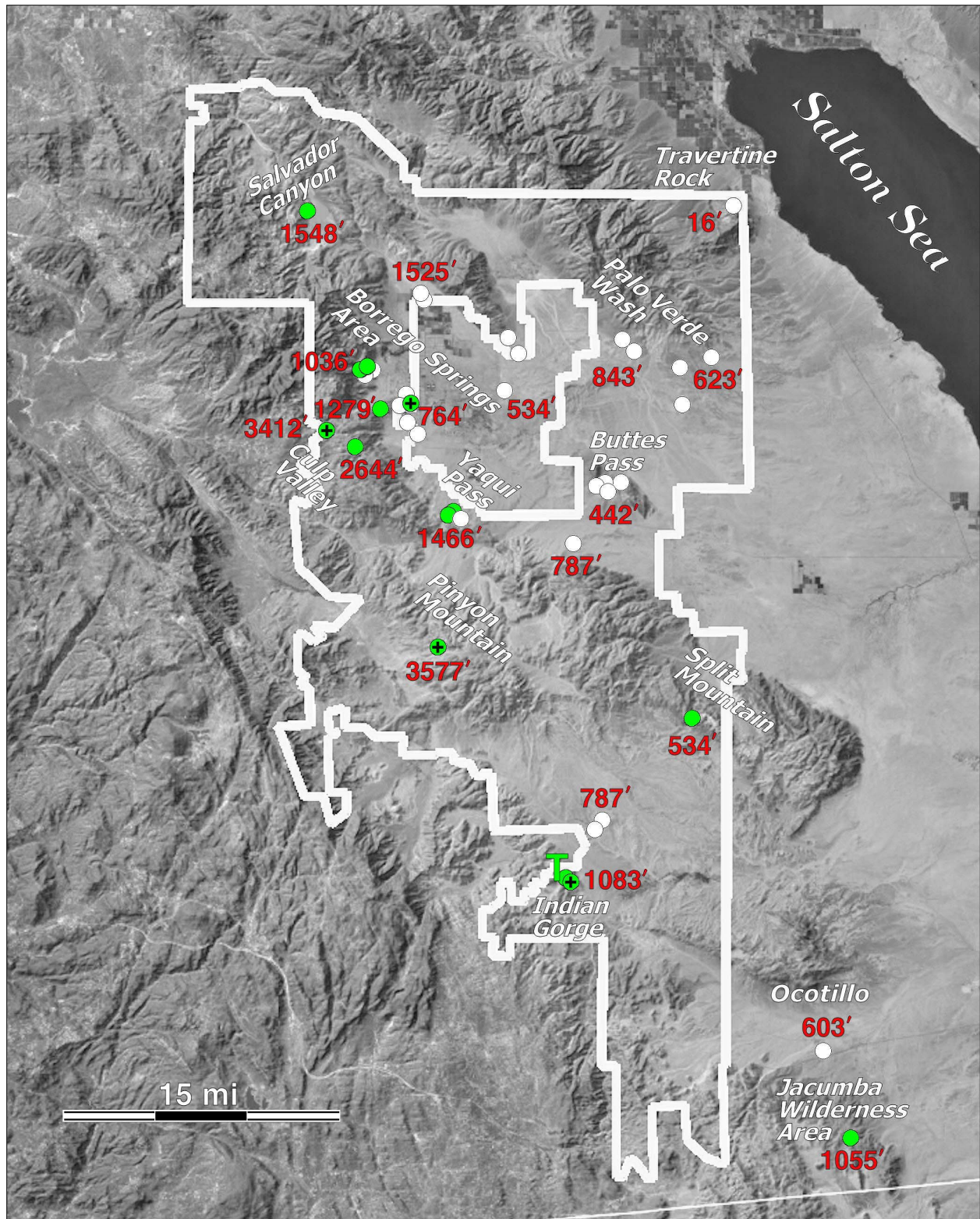
*Hadrurus anzaborrego* is a medium sized species of *Hadrurus*, probably not exceeding 110 mm. This appears to be the case for all members of the “*spadix*” subgroup. Stahnke (1940a: 111), in his original description of *H. spadix*, reported a female of 105.9 mm in length with a carapace of 13 mm, and in his review of



**Figures 50–55:** SEM micrographs of *Hadrurus anzaborrego*, *sp. nov.* **50.** Constellation array showing four sensilla, ABDSP, California. **51–53.** Lateral-ventral view of leg III tarsus showing various development of the fused spinule cluster on different development stages. **51.** Adult, ABDSP, California. **52.** Subadult, Split Mountain, ABDSP, California (carapace = 7.5 mm). **53.** Juvenile, Split Mountain, ABDSP, California (carapace = 4.0 mm). Figs. 50–53 after, in part, Fet et al. (2004, 2006). **54–55.** Basitarsus, left leg I, subadult male paratype showing ventral fused spinule cluster row, Culp Valley Camp, ABDSP, California. **54.** Partial view of row. **55.** Close-up of row showing fused spinules at the base of the spinule clusters.

*Hadrurus* (Stahnke, 1945), two females were reported with lengths of 107.8 mm. Williams (1970: tabs. 3, 9) listed a male *H. spadix* of 108.6 mm. in length and a

female of 107.4 mm long with a carapace of 13.7 mm. Gertsch & Allred (1965: tab. 3) listed a male *H. spadix* 104 mm long with a carapace of 13 mm. Anderson



**Figure 56:** Distribution of *Hadrurus* species in the ABDSP vicinity as referenced in locality data. *H. anzaborrego*, sp. nov., indicated with green icons (type locality marked with green T) and *H. arizonensis arizonensis* indicated with white icons. *H. anzaborrego* localities, from which DNA was analysed, are marked with a "+". Anza-Borrego Desert State Park (ABDSP) outlined in white. Altitudes shown in red.



**Figure 57:** Live photos of *Hadrurus anzaborrego*, *sp. nov.*, male. **Top.** Dark phenotype, Borrego Springs, California, USA. **Bottom.** Light phenotype, Indian Gorge Canyon, ABDSP, California, USA.



**Figure 58:** Live photos of *Hadrurus* species. **Top.** Two pale phenotypes of *H. arizonensis arizonensis*, Borrego Springs, California, USA. **Bottom.** *H. a. arizonensis* (bottom left) and *H. anzaborrego*, *sp. nov.*, pale and dark phenotypes (see Fig. 57 for locality data). Note the pigmented chelal fingers in *H. anzaborrego*, *sp. nov.*, in contrast to the clear fingers in *H. a. arizonensis*.

(1975: tab. 1), who measured 23 male *H. spadix*, reported an average total length of 87.6 mm with a standard deviation of 7.5, indicating a standard error maximum of 95.1 mm. The largest male measured was not indicated. The holotype of *H. obscurus* (Williams, 1970: tab. 9) was listed as 103.7 mm with a carapace of 13 mm. The holotype and paratype females of *H. anzaborrego* measured in this paper are 104.3 mm and 107.9 mm in length and have carapaces of 13.2 mm and 13.55 mm, respectively (see Tab. 2). In contrast, there are many reports of *H. arizonensis arizonensis* exceeding 115 mm: Stahnke (1940a: 107) reported a female of 124.4 mm in length with a carapace of 15.5 mm. In his review of *Hadrurus*, Stahnke (1945: tabs. 2, 3) reported a male 118.5 mm and a female 127.7 mm in length; and Williams (1970: tab. 7) reported a male of 122.3 mm in length. Finally, Williams (1970: tab. 5) reported a male of *H. pinteri* (a member of the “*hirsutus*” group) 119.2 mm in length.

*H. anzaborrego* is found in the Colorado Desert (a subdivision of the greater Sonoran Desert). Its current known range is limited from the northwest by the San Jacinto and Santa Rosa Mountains, from the southwest by the Santa Ana and Laguna Mountains (part of the Peninsular Range), and from the east by the Salton Sea. The range of the new species is separated from that of *H. obscurus*, a Mojave Desert species, on the north by the San Gabriel, San Bernardino, and Little San Bernardino Mountains (part of the Transverse Range). Although almost all records examined in this study are from the ABDSP, two specimens were from elsewhere: one was found to the north, in the extreme southern portion of Joshua Tree National Monument, in Riverside County; another, to the south in the Jacumba Wilderness Area, close to the Mexican border. Williams (1980: fig. 23), in his map of Baja California *Hadrurus* records, shows *H. anzaborrego* (as *H. obscurus*) occurring roughly 40 mi. south into Baja California, on the eastern slopes of the Sierra Juárez (a continuation of the Peninsular Range). Williams (1980) states: “... The Baja California and San Diego County, California, forms are considered here as a geographic race of *H. obscurus* based on a slightly different color pattern of the carapace. ...”.

*Hadrurus anzaborrego* and *H. arizonensis arizonensis* have been collected together at three different localities, two in the Borrego Springs area and one in Yaqui Pass (see map of the ABDSP area in Fig. 56). Both species are burrowers (i.e., fossorial), the latter commonly found at the base of creosote bushes (*Larrea tridentata*) in coarse to soft sandy areas. *H. anzaborrego* frequents areas where the ground cover is coarse sand to gravelly, and usually near rocky areas whereas *H. arizonensis arizonensis* frequents softer sandy areas, often found together with the psammophile *Smeringurus mesaensis* (Stahnke, 1957). The first specimens of *H. anzaborrego* collected by MES (early 1968) were found

by “rock turning” in the Yaqui Pass area. In the ABDSP *H. arizonensis arizonensis* does not occur at the higher altitudes where *H. anzaborrego* can be found. The altitudes reported for *H. arizonensis arizonensis* in our ABDSP material range from 16' near the Salton Sea (which lies below sea level) to 1525' in the Coyote Creek area. *H. anzaborrego* has been collected from as low as 534' in the Borrego Springs and Split Mountain areas to altitudes exceeding 3000', such as the Culp Valley Camp area (3412') and the Pinyon Mountains, (3577').

Collection sites for *H. anzaborrego* span several landscape types (based on macro-, microhabitats and dominant plant communities; Mayer & Laudenslayer, 1988) from the low desert sandy flats, with coarse sand, gravelly surfaces covered with desert scrub; high desert chaparral, with soft to hard soil covered with chamise-redshank chaparral; and the high desert rocky slopes with soft to hard soil with pinyon and juniper as the dominant plants. See four ABDSP collection sites in Figs. 59–60.

Other scorpion species were found at the ABDSP sites where *H. anzaborrego* was collected. We list these species from major ABDSP localities ordered by increasing altitude.

**Split Mountain:** *Smeringurus mesaensis*, *Hoffmannius waeringi* (Williams, 1970), *Kochius hirsuticauda* (Banks, 1910), *Serradigitus joshuaensis* (Soleglad, 1972), *Serradigitus gertschi gertschi* (Williams, 1968), and *Stahnkeus subtilimanus* (Soleglad, 1972).

**Borrego Springs area:** *Hadrurus arizonensis arizonensis*, *Smeringurus mesaensis*, *Hoffmannius waeringi*, *Kochius hirsuticauda*, *Serradigitus joshuaensis*, and *Stahnkeus subtilimanus*.

**Indian Gorge Canyon:** *Hoffmannius waeringi*, *Kochius hirsuticauda*, *Serradigitus joshuaensis*, and *Stahnkeus subtilimanus*.

**Yaqui Pass area:** *Hadrurus arizonensis arizonensis*, *Superstitionia donensis* Stahnke, 1940, *Smeringurus mesaensis*, *Hoffmannius waeringi*, *Kochius hirsuticauda*, and *Serradigitus joshuaensis*.

**Salvador Canyon:** *Smeringurus mesaensis*.

**Culp Valley area:** *Superstitionia donensis*, *Hoffmannius waeringi*, *Kochius hirsuticauda*, and *Serradigitus joshuaensis*.

**Pinyon Mountain:** *Superstitionia donensis*, *Anuroctonus pococki bajaensis* Soleglad et Fet, 2004, *Hoffmannius waeringi*, *Kochius hirsuticauda*, and *Serradigitus joshuaensis*.

### **Phylogeny and biogeography of the “arizonensis” group**

This discussion is based both on morphological and biogeographic considerations. With respect to the former, much of this discussion is based on the detailed cladistic analysis conducted by Fet & Soleglad (2008:



**Figure 59:** Collection localities of *Hadrurus anzaborrego*, **sp. nov.** **Top.** Yaqui Pass Road (1466'), ABDSP, California, USA. **Bottom.** Culp Valley Camp (3412'), ABDSP, California, USA.





**Figure 60:** Collection localities of *Hadrurus anzaborrego*, **sp. nov.** **Top.** Montezuma grade, Culp Valley area (2644'), ABDSP, California, USA. **Bottom.** Hellhole hiking trail (1279'), ABDSP, California, USA.

fig. 26) of the superfamily Iuroidea; individual characters/states from this analysis are referenced where appropriate. And, with respect to this cladistic analysis, the “accessory trichobothria loss” (ATL) hypothesis is invoked where applicable (see Fet & Soleglad, 2004, 2008, for a description of this hypothesis).

Based on the numbers of chelal accessory trichobothria, as well as geographic distribution, we hypothesize that in *Hadrurus* the “*arizonensis*” group is derived, whereas its sister group, the “*hirsutus*” group, occurring in Baja California, is plesiomorphic. From a biogeographic perspective, we consider the “*hirsutus*” group to be plesiomorphic based, in part, on its sole distribution in Baja California. We suggest it represents a primitive form derived from some “protohadurine” existing in mainland Mexico prior to the split of the Baja California peninsula from Mexico (approximately 7 Mya). It is important to note here, taking the ATL hypothesis into consideration, that this presumed plesiomorphic “*hirsutus*” group exhibits accessory trichobothria on three surfaces of the chela, the only clade in subfamily Hadrurinae to do so. Its hypothesized plesiomorphic species, *H. pinteri*, has by far the largest number of accessory trichobothria in the subfamily, exceeding or equaling numbers on all three chelal surfaces of any hadurine species (Soleglad & Fet, 2010). The primary derivations of this derived “*arizonensis*” group are the complete loss of the external accessory trichobothria of the chela (character 39, state = 3, unambiguous synapomorphy) and the loss of the aculear glands on the telson of sexually mature males (character 31, state = 1, homoplastic synapomorphy). As a side note, consistent with this hypothesis, we suggest the mainland Mexican genus *Hoffmannihadrurus* is also derived from the “protohadurine” form and is now represented by its two species in southern Mexico, its most southern species *H. aztecus* being the most recently derived (i.e., it is missing external accessory trichobothria plus has a reduced number of ventral trichobothria). Primary derivations of genus *Hoffmannihadrurus*, among many, are the loss of the internal accessory trichobothria (character 38, state = 4, unambiguous synapomorphy) and the reduction in the fused spinule clusters of the leg tarsus (character 20, state = 3, synapomorphy). Note, based on the above discussion and taking the ATL hypothesis into consideration, we consider *Hoffmannihadrurus* to be derived whereas *Hadrurus* is plesiomorphic.

As indicated in the phylogenetic key, the “*arizonensis*” and “*spadix*” subgroups of the “*arizonensis*” group are sister subgroups. This relationship was demonstrated by the cladistic analysis presented by Fet & Soleglad (2008: fig. 26). These authors also presented a simple area-based cladistic analysis of the unique disjunct distribution of superfamily Iuroidea, and again this relationship was supported. Previously, Fet, Sole-

glad & Barker (2001: figs. 16, 19) also, in part, using molecular information, demonstrated this relationship, in particular with algorithms UPGMA and Direct Optimization combined with morphology. Based on its central distribution and geographic proximity to the “*hirsutus*” group occurring in Baja California, we hypothesize here that the “*arizonensis*” subgroup is the plesiomorphic of the two. This is also indicated by its larger number of accessory trichobothria found on the chela, as discussed above, a corollary of the ATL hypothesis (i.e., in closely related clades, the clade with the larger number of accessory trichobothria is presumed primitive). Primary derived characters for the “*arizonensis*” subgroup are the reduction of the ventral accessory trichobothria (character 40, state = 2, unambiguous synapomorphy) and the development of the crescent-shaped pattern of the carapace anterior edge (character 35, state = 2, potential synapomorphy). For the “*spadix*” subgroup, primary derived characters are the reduction in internal and ventral chela accessory trichobothria (character 38, state = 3, and character 40, state = 5, both unambiguous synapomorphies) and the development of setae between the metasomal ventro-median carinae (character 33, state = 2, unambiguous homoplastic synapomorphy).

Of the three species assigned to the “*spadix*” subgroup (two of which we believe probably are the same species, see discussion above), we propose here that *H. anzaborrego* is likely the most basal taxon in the subgroup. Again, this is based on its larger number of internal accessory trichobothria and likewise close proximity to the center of *H. arizonensis* proposed distribution (i.e., polygons A and B, see map in Fig. 2). This hypothesis would imply, therefore, that *H. obscurus* and *H. spadix* are the most recently evolved species in the “*spadix*” subgroup. In particular, the significant northern radiation of the latter species is certainly consistent with this hypothesis. We suggest here that the split of the “*spadix*” subgroup from the “*arizonensis*” subgroup occurred prior to the latter’s radiation of *H. arizonensis arizonensis*, as indicated by outer polygons C and D (see map in Fig. 2). Primary derivations of *H. obscurus/H. spadix* are the reduction in internal accessory trichobothria and a change to the carapace anterior pattern. We consider the Transverse Mountain Range as a natural barrier between *H. anzaborrego*, a Colorado Desert species, and *H. obscurus* and *H. spadix*, Mojave and Great Basin species.

## Acknowledgments

We thank Anthea Carmichael, Willis J. Gertsch, Matthew R. Graham, Charles Griswold, Gary A. Polis, and Darrell Ubick for the loans and/or gifts of specimens. G. L. thanks Blaine Hébert, Chuck Kristensen, Wendell Icenogle, Stan Williams, Jim and Ellen

Strauss, Jerri Larson, and Russ Bowers for their participation in field trips to collect *Hadrurus*. Special thanks are extended to Matthew R. Graham for providing trichobothria data on his specimens and to Mark Jorgensen (Anza-Borrego Desert State Park, Colorado Desert District) for providing M. S. with a permit to collect scorpions there. We thank David P. A. Neff for his kind help with SEM imaging, and the College of Science, Marshall University, for its constant support of SEM projects. Finally, we extend our gratitude to two anonymous reviewers of this paper.

## References

- ANDERSON, R. C. 1975. Scorpions of Idaho. *Tebiwa*, 18(1): 1–17.
- FET, V., M. S. BREWER, M. E. SOLEGLAD & D. P. A. NEFF. 2006. Constellation array: a new sensory structure in scorpions (Arachnida: Scorpiones). *Boletín de la Sociedad Entomológica Aragonesa*, 38: 269–278.
- FET, V. & M. E. SOLEGLAD. 2005. Contributions to scorpion systematics. I. On recent changes in high-level taxonomy. *Euscorpius*, 31: 1–13.
- FET, V. & M. E. SOLEGLAD. 2008. Cladistic analysis of superfamily Iuroidea, with emphasis on subfamily Hadrurinae (Scorpiones: Iurida). *Boletín de la Sociedad Entomológica Aragonesa*, 43: 255–281.
- FET, V., M. E. SOLEGLAD & M. D. BARKER. 2001. Phylogenetic analysis of the “*hirsutus*” group of the genus *Hadrurus* Thorell (Scorpiones: Iuridae) based on morphology and mitochondrial DNA. Pp. 139–160 in Fet, V. & P. A. Selden (eds.), *Scorpions 2001. In Memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.
- FET, V., M. E. SOLEGLAD, D. P. A. NEFF & I. STATHI. 2004. Tarsal armature in the superfamily Iuroidea (Scorpiones: Iurida). *Revista Ibérica de Aracnología*, 10: 17–40.
- FRANCKE, O. F. & L. PRENDINI 2008. Phylogeny and classification of the giant hairy scorpions, *Hadrurus* Thorell (Iuridae Thorell): a reappraisal. *Systematics and Biodiversity*, 6(2): 205–223.
- FRANCKE, O. F. & M. E. SOLEGLAD. 1981. The family Iuridae Thorell (Arachnida, Scorpiones). *Journal of Arachnology*, 9: 233–258.
- GERTSCH, W. J. & D. M. ALLRED. 1965. Scorpions of the Nevada Test Site. *Brigham Young University Science Bulletin, Biological Series*, 6(4): 1–15.
- HJELLE, J. T. 1972. Scorpions of the Northern Californian coast ranges. *Occasional Papers of the California Academy of Sciences*, 92: 1–59.
- JOHNSON, J. D. & D. M. ALLRED. 1972. Scorpions of Utah. *Great Basin Naturalist*, 32(3): 154–170.
- KOVAŘÍK, F. 1998. *Štíři [Scorpions]*. Jihlava: Madagaskar, 175 pp. (in Czech).
- KOVAŘÍK, F., V. FET, M. E. SOLEGLAD & E. A. YAĞMUR. 2010. Etudes on iurids, III. Revision of the genus *Iurus* Thorell, 1876 (Scorpiones: Iuridae), with a description of two new species from Turkey. *Euscorpius*, 95: 1–212.
- LOWE, G., S. R. KUTCHER & D. EDWARDS. 2003. A powerful new light source for ultraviolet detection of scorpions in the field. *Euscorpius*, 8: 1–7.
- MACMAHON, J. A. 1985. *Deserts*. The Audubon Society Nature Guides. New York: Alfred A. Knopf, 638 pp.
- MAYER, K. E. & W. F. LAUDENSLAYER, JR. (eds.). 1988. *A Guide to Wildlife Habitats of California*. State of California Publication. California Department of Forestry and Fire Protection, Sacramento, CA.
- PRENDINI, L. 2003. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). *American Museum Novitates*, 3408: 1–24.
- PRENDINI, L. & W. C. WHEELER. 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. *Cladistics*, 21: 446–494.
- SHREVE, F. & I. L. WIGGINS. 1964. *Vegetation and Flora of the Sonoran Desert*. Stanford, California: Stanford University Press, 1740 pp.
- SISSOM, W. D. & V. FET. 2000. Family Iuridae Thorell, 1876. Pp. 409–420 in Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998)*. New York, NY: New York Entomological Society, 690 pp.

- SOLEGLAD, M. E. 1976. The taxonomy of the genus *Hadrurus* based on chela trichobothria (Scorpionida: Vejovidae). *Journal of Arachnology*, 3: 113–134.
- SOLEGLAD, M. E. & V. FET. 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni) *Euscorpium*, 5: 1–34.
- SOLEGLAD, M. E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpium*, 11: 1–175.
- SOLEGLAD, M. E. & V. FET. 2008. Contributions to scorpion systematics. III. Subfamilies Smeringurinae and Syntropinae (Scorpiones: Vaejovidae). *Euscorpium*, 71: 1–115.
- SOLEGLAD, M. E. & V. FET. 2010. Further observations on scorpion genera *Hadrurus* and *Hoffmannihadrurus* (Scorpiones: Caraboctonidae). *ZooKeys*, 59: 1–13.
- SOLEGLAD, M. E. & W. D. SISSOM. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. Pp. 25–111 in Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In Memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.
- STAHNKE, H. L. 1940a. *The Scorpions of Arizona* (Ph.D. Dissertation). Ames, Iowa: Iowa State College, 184 pp. (unpublished).
- STAHNKE, H. L. 1940b. The scorpions of Arizona. *Iowa State College Journal of Science*, 15: 101–103.
- STAHNKE, H. L. 1945. Scorpions of the genus *Hadrurus*. *American Museum Novitates*, 1298: 1–9.
- STAHNKE, H. L. 1949 (revised 1956). *Scorpions*. Poisonous Animals Research Laboratory, Arizona State University, Tempe, Arizona. 36 pp.
- STAHNKE, H. L. 1969. Review of *Hadrurus* scorpions (Vejovidae). *Entomological News*, 80(3): 57–65.
- STOCKWELL, S. A. 1989. *Revision of the Phylogeny and Higher Classification of Scorpions (Chelicerata)* (Ph.D. Dissertation). Berkeley, California: University of California, 319 pp. (unpublished). Ann Arbor, Michigan: University Microfilms International.
- VACHON, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (3), mai-juin 1973, 140 (Zool. 104): 857–958.
- VOLSCHENK, E. S. 2005. A new technique for examining surface morphosculture of scorpions. *Journal of Arachnology*, 33: 820–825.
- WILLIAMS, S. C. 1970. A systematic revision of the giant hairy scorpion genus *Hadrurus*. *Occasional Papers of the California Academy of Sciences*, 87: 1–62.
- WILLIAMS, S. C. 1980. Scorpions of Baja California, Mexico and adjacent islands. *Occasional Papers of the California Academy of Sciences*, 135: 1–127.