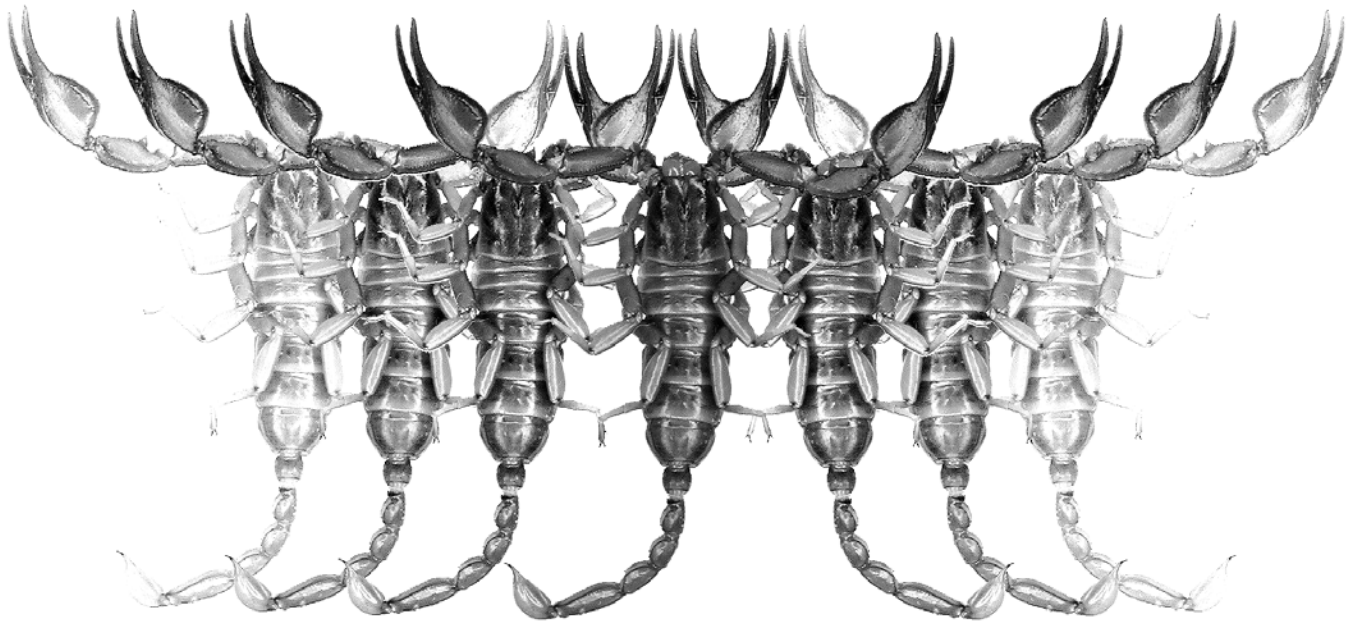


Euscorpius

Occasional Publications in Scorpiology



**Contributions to Scorpion Systematics. IV. Observations
on the *Hadrurus* “*spadix*” Subgroup with a Description
of a New Species (Scorpiones: Caraboctonidae)**

Michael E. Soleglad, Victor Fet & Graeme Lowe

February 2011 — No. 112

Euscorpius

Occasional Publications in Scorpiology

EDITOR: Victor Fet, Marshall University, 'fet@marshall.edu'

ASSOCIATE EDITOR: Michael E. Soleglad, 'soleglad@la.znet.com'

Euscorpius is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). *Euscorpius* takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). *Euscorpius* is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

Derivatio Nominis

The name *Euscorpius* Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

Euscorpius is located on Website '<http://www.science.marshall.edu/fet/euscorpius/>' at Marshall University, Huntington, WV 25755-2510, USA.

The International Code of Zoological Nomenclature (ICZN, 4th Edition, 1999) does not accept online texts as published work (Article 9.8); however, it accepts CD-ROM publications (Article 8). *Euscorpius* is produced in two *identical* versions: online (ISSN 1536-9307) and CD-ROM (ISSN 1536-9293). Only copies distributed on a CD-ROM from *Euscorpius* are considered published work in compliance with the ICZN, i.e. for the purposes of new names and new nomenclatural acts. All *Euscorpius* publications are distributed on a CD-ROM medium to the following museums/libraries:

- **ZR**, Zoological Record, York, UK
- **LC**, Library of Congress, Washington, DC, USA
- **USNM**, United States National Museum of Natural History (Smithsonian Institution), Washington, DC, USA
- **AMNH**, American Museum of Natural History, New York, USA
- **CAS**, California Academy of Sciences, San Francisco, USA
- **FMNH**, Field Museum of Natural History, Chicago, USA
- **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, USA
- **MNHN**, Museum National d'Histoire Naturelle, Paris, France
- **NMW**, Naturhistorisches Museum Wien, Vienna, Austria
- **BMNH**, British Museum of Natural History, London, England, UK
- **MZUC**, Museo Zoologico "La Specola" dell'Universita de Firenze, Florence, Italy
- **ZISP**, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
- **WAM**, Western Australian Museum, Perth, Australia
- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway
- **OUMNH**, Oxford University Museum of Natural History, Oxford, UK
- **NEV**, Library Netherlands Entomological Society, Amsterdam, Netherlands

Publication date: 2 February 2011

Contributions to scorpion systematics. IV. Observations on the *Hadrurus* “*spadix*” subgroup with a description of a new species (Scorpiones: Caraboctonidae)

Michael E. Soleglad¹, Victor Fet², and Graeme Lowe³

¹ P.O. Box 250, Borrego Springs, California 92004, USA; email: soleglad@znet.com

² Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755-2510, USA; email: fet@marshall.edu

³ Monell Chemical Senses Center, 3500 Market St., Philadelphia, Pennsylvania 19104-3308, USA; email: loweg@monell.org

Summary

In this study new data are presented on the “*spadix*” subgroup of genus *Hadrurus*, including the description of a new species, *H. anzaborrego*, **sp. nov.**, found primarily in the Anza-Borrego Desert State Park (ABDSP) in southern California, USA. This species is distinguished by its internal trichobothrial pattern of the chela and its unique carapace pattern. The status of *Hadrurus obscurus* Williams, 1970 is discussed and new locality data for this species are provided. A phylogenetic key to the genera, species, and subspecies of subfamily Hadrurinae is provided.

Introduction

The first species in the *Hadrurus* “*spadix*” subgroup was named by H. L. Stahnke (1940b; also in 1940a: 107–111 [unpublished]) when he described *Hadrurus spadix* from northern Arizona. *H. spadix* was referenced again by Stahnke (1945, 1969) in two papers; during the same period, Stahnke (1949) also published a photograph of *H. spadix*, probably the first published of this species, in his popular pamphlet on scorpions (photo replicated in our Fig. 1). *H. spadix* was reported from Nevada by Gertsch & Allred (1965), from Utah by Johnson & Allred (1972), and from Idaho by Anderson (1975). Williams (1970) included a detailed description and distribution map of *H. spadix* in his excellent revision of the genus. The other species in the *Hadrurus* “*spadix*” subgroup, *H. obscurus*, was described by Williams in 1970. Hjelle (1972) also referenced *H. obscurus* in his paper on the scorpions of northern California but did not report new localities, listing only the original type locality as reported by Williams (1970). Soleglad (1976: figs. 22–25, 28) presented for the first time the chelal trichobothria pattern of the *Hadrurus* “*spadix*” subgroup.

When Soleglad (1976) published the chelal trichobothria patterns for genus *Hadrurus*, he included a southern population of *H. obscurus* in his data, considerably south of its then known distribution. At that time, Soleglad (1970: 114) wrote:

“... With the possible exception of *H. obscurus* Williams, each species or subspecies was well represented with respect to geographical range. All *H. obscurus* specimens were from Southern California, somewhat south of its recorded range (Williams, 1970, and Hjelle, 1972); the northern most sample came from the southern portion of Joshua Tree National Monument. The other specimens sampled were from the Anza-Borrego State Park or further south, approaching the Mexican border....”.

Based on new trichobothria data on *H. obscurus* and the examination of populations south of its reported range, we have come to the conclusion that the southern population from the Anza-Borrego Desert State Park is a different species altogether and therefore new. New species *Hadrurus anzaborrego*, **sp. nov.**, is described and the status of *H. obscurus* is discussed, where evidence suggests that it may only be a color-variant phenotype of *H. spadix* Stahnke, 1940.

Below we provide a phylogenetic key to subfamily Hadrurinae followed by a short synopsis of each taxon. Discussions on the diagnostic differences between the “*arizonensis*” and “*spadix*” subgroups as well as the species in the “*spadix*” subgroup are presented. An overview of the Fet, Soleglad & Barker (2001) molecular analysis of genus *Hadrurus* with an emphasis on the “*arizonensis*” group is provided, followed by the description of new species *Hadrurus anzaborrego*. Finally, phylogenetic and biogeographic observations

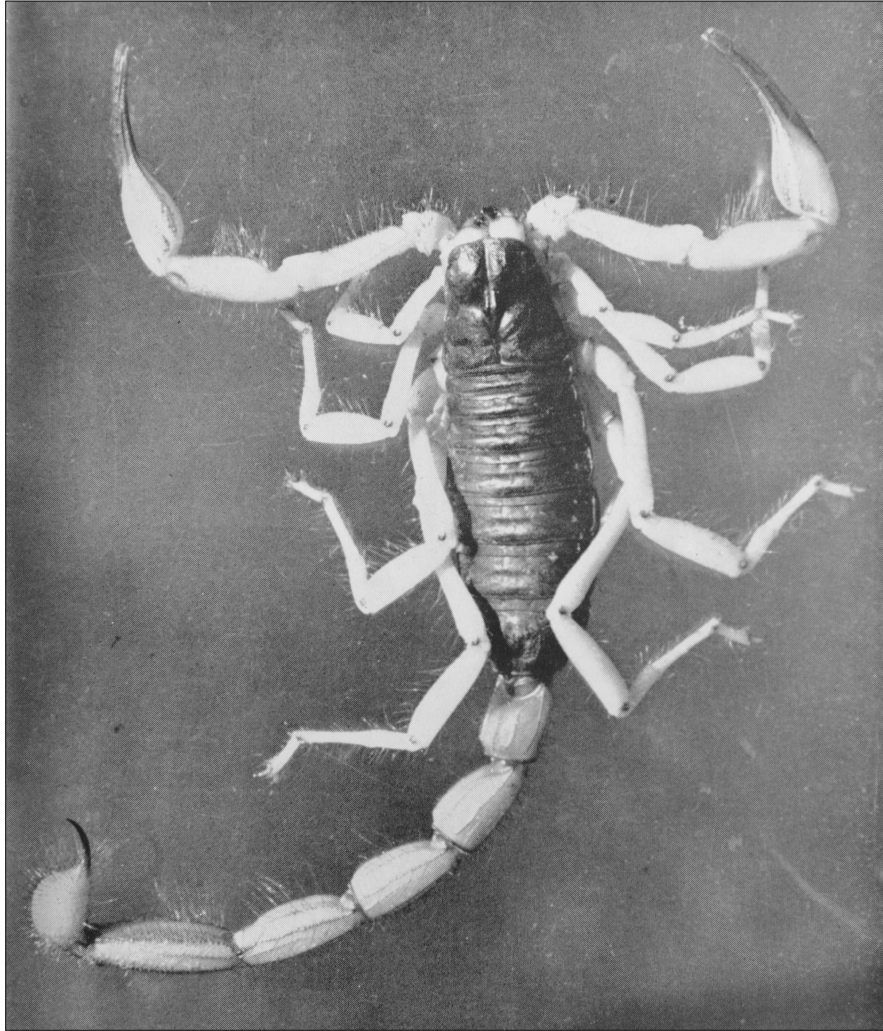


Figure 1: Photo of *Hadrurus spadix* Stahnke, 1940, from Herbert Stahnke's popular pamphlet on scorpions, "Scorpions" (1949), inside back cover.

for the "*arizonensis*" group are presented, factoring in the cladistic analysis results of Fet & Soleglad (2008).

Informal taxonomic grouping in *Hadrurus*

"Species groups" (complexes) or even further "subgroups" are sometimes used in scorpion genera where a recognition of categories such as subgenus has not been common. Such informal groupings, to some extent, reflect phylogenetic relationships within a genus, and must be taken into account in further phylogenetic analyses. The first taxonomic partitioning of the "giant hairy-scorpion" *Hadrurus* was presented by Williams (1970) in his extensive revision of the genus. In his study, *Hadrurus* was divided into three informal "subgroups": (a) one mainland Mexican species *Hadrurus aztecus* Pocock, 1902 (now placed in genus *Hoffmannihadrurus*); (b) three Baja California (Mexico) species: *Hadrurus hirsutus* (Wood, 1863), *H. concolorous* Stahnke, 1971, and *H. pinteri* Stahnke, 1971;

and (c) three species occurring primarily in the United States, *H. arizonensis* Ewing, 1928, *H. spadix* Stahnke, 1940, and *H. obscurus* Williams, 1970.

Soleglad (1976), using neobothriotaxy of the pedipalp chela as a taxonomic character, which endorsed Williams's suggested phylogeny, broke *Hadrurus* into two "groups", the "*aztecus*" group (to which *Hadrurus gertschi* Soleglad, 1976, now placed in *Hoffmannihadrurus*, was added) and the "*hirsutus*" group. Each group was split into two "subgroups". These distinctions were based, in most part, on the presence/absence of neobothriotaxy on the chela as well as the number of accessory trichobothria. Many years later, Fet, Soleglad & Barker (2001) presented a molecular- and morphology-based cladistic analysis of genus *Hadrurus*. In this paper, details were provided on the coloration and patterns of these species, using the term "complex" for these subdivisions.

While the southern Mexican species are now recognized as quite distinct from the United States and Baja

California species and therefore placed in a separate genus *Hoffmannihadrurus* (Fet et al., 2004; Fet & Soleglad, 2008; Soleglad & Fet, 2010), the remaining species of genus *Hadrurus* can be partitioned into informal taxonomic “groups” and “subgroups”, terms used in this paper.

Material and Methods

Abbreviations

List of depositories: GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA.

Other: ABDSP, Anza-Borrego Desert State Park, San Diego and Riverside Counties, California, USA.

Terminology and conventions

The systematics adhered to in this paper follows the classification as established in Fet & Soleglad (2005) and as modified in Fet & Soleglad (2008). Terminology describing pedipalp chelal finger dentition follows that described and illustrated in Soleglad & Sissom (2001), that of the sternum follows Soleglad & Fet (2003a), and the metasomal and pedipalp carination, and leg tarsus armature follows Soleglad & Fet (2003b). Hemispermatophore terminology is from Soleglad & Fet (2008) and Kovářik et al. (2010). Trichobothrial nomenclature and hypothesized homologies are those described and illustrated in Vachon (1974) and Soleglad (1976). Techniques using maximized morphometric ratios follow those described in Kovářik et al. (2010).

References to the *Colorado Desert* in this paper apply to the geographic area addressed as “the Lower Colorado Valley”, in part, by Shreve & Wiggins (1964: map 1) and the “Salton Trough” by MacMahon (1985: 34).

SEM microscopy

To investigate *Hadrurus* morphology, various structures of specimens kept in 70 % ethanol were air-dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. Digital SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia. Acceleration voltage (10–20 kV), spot size, and working distance were adjusted as necessary to optimize resolution, adjust depth of field, and to minimize charging.

UV photography

Images of chelal trichobothria patterns were acquired by UV epifluorescence imaging (Prendini, 2003;

Volschenk, 2005). Scorpions were illuminated by a primary 198 UV LED array (395 nm), with a secondary 168 UV LED array used for fill lighting (Lowe, Kutcher & Edwards, 2003). A vertical translation stage (Ealing) was used to adjust specimen position. Images were acquired at a series of focal planes with a Canon EOS 7D camera, and MP-E 65 mm macro lens with long pass filter (475 nm), and combined with Zerene Stacker software (Zerene Systems, LLC).

Map generation

Maps were generated from Earth Explorer 6.1, with positional and altitude data compiled through Google Maps and Topo! Interactive Maps for the San Diego, San Jacinto Wilderness, and Anza-Borrego Desert areas.

Material examined

The following material of the *Hadrurus* “*arizonensis*” group was examined and/or contributed to the statistical data presented in this paper (430 specimens). In particular, the material from the Anza-Borrego Desert State Park area was collected by the first author throughout the years from 1968 to the present. Exact positional data is presented as (latitude (N), -longitude (W); elevation a.s.l. (feet))

Hadrurus “*arizonensis*” subgroup

Hadrurus arizonensis arizonensis Ewing, 1928 (282 specimens):

Mexico. Baja California: 3 mi. N of San Felipe (31.051, -114.872; 177'), 2 juvenile ♂, 5 April 1969 (M. Soleglad) (MES); 5.5 mi. N of San Felipe (31.079, -114.884; 152'), 1 adult ♂, 29 May 1971 (M. Soleglad) (MES); 5 mi. N of San Felipe (31.074, -114.881; 136'), 2 juvenile ♂, 1 adult ♀, 3 May 1975 (M. Soleglad) (MES); 5 mi. N of Puertocitos (30.416, -114.643; 61'), 1 subadult ♂, 3 adult ♀, 2 subadult ♀, 1 juvenile ♀, 25 May 1974 (M. Soleglad) (MES); 25.1 mi. N of Puertocitos (30.723, -114.718; 42'), 4 adult ♂, 2 subadult ♂, 7 juvenile ♂, 2 adult ♀, 1 subadult ♀, 6 juvenile ♀, 26 July 1975 (M. Soleglad) (MES). **Sonora:** Mex-2, 66 mi. W of Sonoyta (32.148, -113.942; 1226'), 2 adult ♀, 4 September 1971 (M. Soleglad) (MES); Puerto Peñasco (31.309, -113.538; 33'), 5 adult ♂, 1 subadult ♂, 2 juvenile ♂, 2 adult ♀, 1 subadult ♀, 4 September 1971 (M. Soleglad), 1 juvenile ♂, 1 adult ♀, 3 subadult ♀, 1 juvenile ♀, 28 March 1970 (M. Soleglad) (MES); 11 mi. S of Guaymas (27.956, -110.779; 28'), 1 subadult ♂, 1 juvenile ♂, 2 adult ♀, 1 subadult ♀, 3 juvenile ♀, 13 July 1973 (M. Soleglad) (MES); Mex-2, 41.2 mi. E of San Luis (32.291, -114.147; 761'), 4 adult ♂, 1 subadult ♂, 2 juvenile ♂, 3 adult ♀, 1 subadult ♀, 1 juvenile ♀, 11 July 1973 (M. Soleglad) (MES).

USA. Arizona: Maricopa County: 5 mi. NE of Mesa (33.477, -111.716; 1387'), 7 adult ♂, 10 subadult ♂, 3 juvenile ♂, 5 adult ♀, 17 subadult ♀, 6 juvenile ♀, 3-4 July 1970 (M. Soleglad) (MES); 10 mi. NE of Mesa (33.551, -111.579; 1435'), 6 adult ♂, 4 juvenile ♂, 3 adult ♀, 5 subadult ♀, 5 juvenile ♀, 3-4 July 1970 (M. Soleglad) (MES). **California: Imperial County:** Picacho Recreation Area, 23 mi. N of Winterhaven (32.923, -114.472; 183'), 1 adult ♂, 1 subadult ♂, 1 adult ♀, 1 subadult ♀, 28 February 1970 (M. Soleglad), 5 subadult ♂, 1 juvenile ♂, 2 adult ♀, 1 subadult ♀, 24 April 1970 (M. Soleglad), 1 adult ♂, 1 subadult ♂, 1 adult ♀, 1 subadult ♀, 15 August 1970 (M. Soleglad), 3 adult ♀, 16 May 1971 (M. Soleglad) (MES); 3 mi. NW of Ocotillo (32.751, -116.038; 603'), 1 subadult ♂, 2 subadult ♀, 3 February 1968 (M. Soleglad), 1 subadult ♂, 2 subadult ♀, 2 September 1968 (M. Soleglad) (MES). **Inyo County:** Tecopa Hot Springs, Old Spanish Trail, 0.8 mi. off Rte. 127 (35.848, -116.226; 1341'), 1 adult ♂, 19 July 1985 (G. Lowe, B. Hébert) (GL); Rte 178, 0.5 W Rte 127 (35.997, -116.284; 1690'), 2 juvenile ♂, 20 July 1985 (G. Lowe, B. Hébert) (GL). **Los Angeles County:** Rocky Buttes, Antelope Valley, 0.5 mi. S M Ave/150th St. (34.647, -117.872; 2657'), 1 adult ♂, 3 July 1987 (G. Lowe, B. Hébert) (GL); E-side Lovejoy Buttes and Rawhide St. (34.600, -117.857; 3036'), 1 adult ♂, 22 July 1985 (G. Lowe, B. Hébert) (GL). **Riverside County:** 2.5 mi SE Cabazon (33.891, -116.756; 1679'), 2 adult ♂, 17 September 1983 (G. Lowe, C.P. Kristensen) (GL); 1.2 mi. N of Varner and Rio Del Sol, near Thousand Palms (33.839, -116.411; 401'), 1 adult ♂, 31 January 1970 (M. Soleglad), 1 adult ♀, 11 April 1970 (M. Soleglad), 1 subadult ♂, 2 adult ♀, 2 subadult ♀, 15 May 1970 (M. Soleglad), 1 adult ♂, 1 juvenile ♂, 1 adult, 1 juvenile ♀, 17 October 1970 (M. Soleglad), 1 subadult ♂, 23 March 1971 (M. Soleglad), 2 subadult ♂, 28 August 1971 (M. Soleglad) (MES); Cottonwood Springs, Joshua Tree National Monument (33.743, -115.815; 3068'), 1 subadult ♂, 1 juvenile ♂, 3 May 1970 (M. Soleglad), 1 subadult ♂, 1 juvenile ♂, 6 September 1970 (M. Soleglad) (MES). **San Bernardino County:** 1 mi. N of Saratoga Springs, Death Valley National Monument (35.735, -116.385; 740'), 1 subadult ♀, 23 October 1971 (M. Soleglad) (MES). **San Diego County:** 3 mi. NE of Borrego Springs (33.255, -116.291; 534'), 2 juveniles, 2 September 1968 (M. Soleglad), 2 ♂, 26 June 1970 (M. Soleglad) (MES); Carrizo Badlands, 1 mi. E of Palm Springs, ABDSP (32.919, -116.201; 902'), 1 ♀, 7 November, 1970 (M. Soleglad) (MES); Borrego Badlands, 1 mi. SW of Seventeen Palms Oasis, ABDSP (33.245, -116.123, 462'), subadult ♀, 12 June 1971 (M. Soleglad), 1 subadult ♀, 14 August 1971 (M. Soleglad) (MES); Coyote Creek, 10 mi. NW Borrego Springs, ABDSP (33.399, -116.462; 1525'), 1 April 1972, 2 subadult ♂, 1 juvenile ♂, 2 subadult ♀, 1 juvenile ♀ (M. Soleglad), 29 July 1972, 5 ♂ (M. Soleglad) (MES); DiGiorgio Road/ Coyote Creek juncture, ABDSP (33.329, -116.368; 731'), 2 subadult ♂, 1 subadult ♀, 13 July 1996 (M. Soleglad) (MES); 0.25 mi. N of Salton Sea Expressway, Rd to Clark's Dry Lake, ABDSP (33.297, -116.287; 652'), 1 subadult ♂, 21 July 1996 (M. Soleglad) (MES); Borrego Badlands, Buttes Pass, 0.3 mi. N Hawk's Canyon exit, ABDSP (33.183, -116.199; 603'), 1 ♂, 1 ♀, 22 July 1996 (M. Soleglad) (MES); Borrego Badlands, Palo Verde Wash entry, off Salton Sea Expressway, ABDSP (33.295, -116.181; 843'), 1 ♂, 1 ♀, 5 August 1996 (M. Soleglad), 1 ♂, 1 ♀, 19 October 1998 (M. Soleglad), 1 ♂, 14 July 1999 (M. Soleglad) (MES); Borrego Badlands, Arroyo Salado, 1.5 mi. S of Salton Sea Expressway, ABDSP (33.274, -116.128; 623'), 1 subadult ♂, 1 juvenile ♂, 2 subadult ♀, 2 juvenile ♀, 7 August 1996 (M. Soleglad) (MES); Borrego Badlands, Hawk's Canyon, ABDSP (33.181, -116.205; 800'), 1 subadult ♂, 20 August 1996 (M. Soleglad) (MES); Borrego Badlands, Buttes Pass, 0.5-1.5 mi. N Hawk's Canyon exit, ABDSP (33.178, -116.194; 442'), 1 juvenile ♀, 27 August 1997 (M. Soleglad) (MES); Country Club and Borrego Springs Roads, Borrego Springs (33.242, -116.376; 600'), 3 subadult ♂, 1 adult ♂, 2 subadult ♀, 2 juvenile ♀, 3 September 1996 (M. Soleglad) (MES); Borrego Badlands, Blow Sand Canyon, 1 mi. S of San Felipe Wash, ABDSP (33.183, -116.182; 433'), 1 juvenile ♀, 5 November 1996 (M. Soleglad), 1 juvenile ♀, 2 June 1997 (M. Soleglad) (MES); Palm Canyon Hiking Trail, primary trail, ABDSP (33.273, -116.423; 915'), 3 subadult ♂, 1 juvenile ♂, 1 subadult ♀, 10 March 1997 (M. Soleglad) (MES); Borrego Badlands, Calcite Mine area (just N. of S-22), ABDSP (33.283, -116.098; 561'), 1 ♂, 1 subadult ♀, 1 juvenile ♀, 29 April 1997 (M. Soleglad) (MES); Cactus Garden, 2.2 mi. S HWY-78, ABDSP (33.136, -116.226, 787'), 3 subadult ♂, 1 juvenile ♂, 2 subadult ♀, 1 juvenile ♀, 13 May 1997 (M. Soleglad) (MES); Coyote Creek Road, 0.2 mi. N of DiGiorgio Road, ABDSP (33.332, -116.369; 741'), 1 subadult ♂, 27 May 1997 (M. Soleglad) (MES); 1.65 mi. W of Travertine Rock (off HWY-86), ABDSP (33.400, -116.077; 16'), 1 adult ♂, 1 juvenile ♂, 1 adult ♀, 26 August 1997 (M. Soleglad) (MES); Borrego Badlands, Palo Verde Wash, 1.2 mi. S of Salton Sea Expressway, ABDSP (33.284, -116.279; 757'), 1 adult ♂, 1 subadult ♂, 1 adult ♀, 12 September 1997 (M. Soleglad) (MES); Carrizo Badlands, Vallecito Creek, 3.3 mi. E S-2, ABDSP (32.910, -116.206; 787'), 1 adult ♂, 1 juvenile ♂, 1 subadult ♀, 1 juvenile ♀, 2 October 1997 (M. Soleglad) (MES); Borrego Badlands, Palo Verde Wash, 1 mi. S of Salton Sea Expressway, ABDSP (33.286, -116.170; 774'), 1 ♂, 20 July 1998 (M. Soleglad) (MES); Borrego Springs area, Montezuma Grade, 0.5 mi. from S-22, ABDSP (33.250, -116.380; 656'), 1 ♂, 3 August 1998 (M. Soleglad) (MES); West Star Road, Borrego Springs (33.230, -116.381; 692'), 1 ♂, 13 October 1998 (M. Soleglad) (MES); W end of Tilting-T, Borrego Springs (33.242, -116.388; 764'), 1 ♂, 15 October 1998 (M. Soleglad)

(MES); W end of Weather Vane, Borrego Springs (33.245, -116.380; 585'), 1 ♂, 12 September 2010 (M. Soleglad) (MES).

***Hadrurus arizonensis austrinus* Williams, 1970 (13 specimens):**

Mexico. Baja California: Oakies Landing (30.052, -114.584; 15'), 1 adult ♀, 1 juvenile ♀, 26 May 1974 (M. Soleglad), 1 adult ♂, 2 juvenile ♂, 3 adult ♀, 3 subadult ♀, 2 juvenile ♀, 27 July 1975 (M. Soleglad) (MES).

***Hadrurus "spadix"* subgroup**

***Hadrurus anzaborrego* Soleglad, Fet et Lowe, sp. nov. (51 specimens, including holotype and 19 paratypes; see below):**

USA. California: Riverside County: 1 mi. S of Cottonwood Springs, Joshua Tree National Monument (33.731, -115.813; 2988'), 1 adult ♂, 26 June 1971 (M. Soleglad) (MES). **San Diego County:** 0.25 mi. SE of Salvador Canyon, off Coyote Creek, ABDSP (33.396, -116.476; 1548'), 1 subadult ♀, 27 April 1974 (M. Soleglad) (MES); Culp Valley Camp, ABDSP (33.224, -116.460; 3412'), 3 subadult ♂, 1 adult ♀, 2 subadult ♀, 1 juvenile ♀, 23 July 1996 (M. Soleglad), 1 adult ♂, 27 August 1998 (M. Soleglad) (MES); Montezuma Grade, in Culp Valley area, 2.1 mi. E of Culp Valley Camp, ABDSP (33.211, -116.431; 2644'), 1 subadult ♂, 5 September 1996 (M. Soleglad) (MES); Hellhole Hiking Trail, 1–2 mi. W of Montezuma Grade, ABDSP (33.241, -116.408; 1279'), 1 subadult ♂, 1 subadult ♀, 29 July 1996 (M. Soleglad) (MES); Palm Canyon Hiking Trail, alternate back trail, ABDSP (33.271, -116.424; 997'), 1 subadult ♂, 14 September 1996 (M. Soleglad) (MES); Palm Canyon Hiking Trail, primary trail, ABDSP (33.272, -116.425; 1036'), 1 subadult ♂, 1 adult ♀, 1 juvenile ♀, 16 April 1997 (M. Soleglad) (MES); Borrego Springs area, W end of Tilting T Road, ABDSP (33.242, -116.388; 764'), 1 adult ♀, 5 March 1997 (M. Soleglad), 1 adult ♀, 15 October 1998 (M. Soleglad), 1 adult ♂, 14 July 1999 (M. Soleglad) (MES); Yaqui Pass Road, 3 mi. N of HWY-78, ABDSP (33.159, -116.342; 1466'), 1 adult ♂, 1 adult ♀, 2 juvenile ♀, 16 March 1968 (M. Soleglad) (MES); Yaqui Pass Road, 3.2 mi. N of HWY-78, ABDSP (33.160, -116.340; 1437'), 3 adult ♂, 3 subadult ♂, 1 adult ♀, 1 subadult ♀, 26 June 1970 (M. Soleglad), 2 adult ♂, 1 subadult ♂, 2 adult ♀, 1 subadult ♀, 23 October 1970 (M. Soleglad), 2 adult ♂, 1 adult ♀, 17 July 1996 (M. Soleglad) (MES); Pinyon Mountain Road, 4.3 mi. E. HWY-S2, ABDSP (33.054, -116.353; 3577'), 1 adult ♀, 4 June 1997 (M. Soleglad), 1 adult ♂, 1 subadult ♀, 20 July 1999 (M. Soleglad) (MES); Split Mountain, ABDSP (32.999, -116.116; 534'), 2 ♂, 1 adult ♀, April 28, 1997 (M. Soleglad) (MES); Indian Gorge Canyon, 1.7 mi. W. S-2, ABDSP (32.874, -116.235; 1083'), 2 adult ♀, 22 June 1998 (M. Soleglad) (MES); Indian Gorge Canyon, 1.4 mi.

W. S-2, ABDSP (32.871, -116.230; 1003'), 1 adult ♂, 15 July 1999 (M. Soleglad) (MES). **Imperial County:** Jacumba Wilderness Area, 2.9 mi. SW of HWY-98 (6.3 S of HWY-8) (32.669, -115.969; 1055'), 1 subadult ♂, 26 February 1972 (M. Soleglad) (MES).

***Hadrurus obscurus* Williams, 1970 (18 specimens):**

California: Kern County: Jawbone Canyon Road (35.321, -118.112; 2896'), 1 adult ♂, 1 August 1997 (G. Lowe, B. Hébert) (GL); Jawbone Canyon Road (35.318, -118.082; 2,630'), 3 adult ♂, 1 adult ♀, 1 subadult ♀, 1–2 August 1997 (G. Lowe, B. Hébert) (GL); Nine Mile Canyon Road (35.846, -117.947; 4,222'), 1 juvenile ♂, 2 August 1997 (G. Lowe, B. Hébert) (GL); Nine Mile Canyon Road (35.856, -118.027; 6,485'), 1 adult, 1 juvenile ♂, 2 August 1997 (G. Lowe, B. Hébert) (GL); Nine Mile Canyon Road (35.858, -117.997; 5,978'), 1 adult ♂, 2 August 1997 (G. Lowe, B. Hébert) (GL); Bird Spring Canyon Road (35.547, -118.132; 5,241'), 1 adult ♂, 1 subadult ♀, 3 August 1997 (G. Lowe, B. Hébert) (GL); Antelope Valley, SE Mohave (34.950, -118.287; 2,976'), 1 adult ♂, 5 August 1997 (G. Lowe, B. Hébert) (GL). **Los Angeles County:** Cheseboro Rd., 0.25 mi. S of Aqueduct, 4.5 mi SE of Palmdale (34.518, -118.028; 2949'), 2 adult ♂, 7 June 1985 (G. Lowe, B. Hébert) (GL); Edwards Airforce Base (34.789, -118.114; 2284'), 2 juvenile ♂, 4 October 1980 (G. Lowe, J. & E. Strauss) (GL); Pearblossom Hwy, Rte. 135, 0.85 mi. SE junction of Ave T, S of Palmdale (34.535, -118.018; 2804'), 1 adult ♂, 7 June 1985 (G. Lowe, B. Hébert) (GL).

***Hadrurus spadix* Stahnke, 1940 (66 specimens):**

General localities used in trichobothrial analysis (Soleglad, 1976; Fet, Soleglad & Barker, 2001): **Arizona: Coconino County:** Grand Canyon, 1 specimen, Wupatki National Monument, 4 specimens. **Idaho: Elmore County:** Mountain Home, 5 specimens. **Owyhee County:** Hammet State Park, 1 specimen, Hot Creek Falls, 27 specimens. **Nevada: Humboldt County:** Winnemucca, 2 specimens. **Mineral County:** Hawthorne, 1 specimen. **Nye County:** Mercury, 1 specimen. **Oregon: Malheur County:** 1 specimen. **Utah: Grand County:** Moab, 2 specimens, area of HWY-128/HWY-6 intersection, 13 specimens. **San Juan County:** Bluff, 1 specimen.

Specimens examined in this study: **California: Inyo County:** 3.4 SSW Towne Pass, Panamint Range (36.393, -117.279; 4935'), 1 adult ♀, 27 July 1987 (G. Lowe, C. R. Bowers) (GL); Eureka Dune (37.085, -117.674; 3043'), 1 adult ♂, 20 August 1990 (G. Lowe, S. C. Williams, et al.) (GL); **San Bernardino County:** HWY 15/Cima road intersection (35.444, -115.675; 3730'), 1 subadult ♂, 1 July 1984 (G. Lowe, J. Larson et al.) (GL). **Nevada: Lincoln County:** 4 mi. E Elgin (37.351, -114.442; 5204'), 1 adult ♀, 17 August 1998 (G. Lowe, S. C. Williams, V. F. Lee, J. S. Chinn) (GL);

Mineral County: 3.3 km N Thorne (38.633, -118.596; 4520'), 1 adult ♂, 10 August 1990 (G. Lowe, S. C. Williams, et al.) (GL); **Utah: San Juan County:** Valley of the Gods (37.276, -109.867; 4704'), 1 adult ♂, 20 September 2004 (G. Lowe) (GL). **Washington County:** Apex Mine, Curly Hollow Wash (37.070, -113.724; 3341'), 1 adult ♂ (G. Lowe, W. Icenogle) (GL).

Systematics

For details on the phylogenetic characters supporting the hadrurine topology in the following key refer to Fet & Soleglad's (2008) cladistic analysis of superfamily Iuroidea and the recent contribution by Soleglad & Fet (2010) on *Hadrurus pinteri* Stahnke. Also refer to the discussion on phylogeny and biogeography at the end of this paper. Species level distinctions refer to typical and/or statistically dominant characters, therefore some minor exceptions may exist, see discussions below. Numerical ranges are defined as minimum–maximum (mean).

Phylogenetic key to genera, species, and sub-species of subfamily Hadrurinae

- 1:** Internal accessory trichobothria absent on chela, trichobothria *ib–it* positioned basally on the fixed finger; dorsosecondary (*D3*) and dorsomarginal (*D4*) carinae of chela not rounded basally but discretely formed, not covered with coarse granulation, intercarinal area wide, distinct and smooth; patellar proximal area with conspicuous projection; extreme carapace anterior edge considerably convex, *anterior edge length / median tubercle position* ratio 0.327–0.383 (0.354); leg tarsus and basitarsus with weak or obsolete ridges on fused spinule clusters (genus *Hoffmannihadrurus* Fet et Soleglad, 2004) **2**
- : 2–7 internal accessory trichobothria present on chela, trichobothria *ib–it* positioned suprabasally on the fixed finger; *D3* and *D4* carinae of chela rounded basally, covered with coarse granulation, intercarinal area narrow due to dense granulation; patellar proximal area essentially flat; extreme carapace anterior edge modestly convex, *anterior edge length / median tubercle position* ratio 0.206–0.267 (0.240); leg tarsus and basitarsus with well developed ridges on fused spinule clusters (genus *Hadrurus* Thorell, 1876) **3**
- 2:** 3–4 external accessory trichobothria present on chela; 20–25 (21.143) ventral trichobothria present on chela; aculear glands absent on telson in mature male; pedipalps, metasoma, and telson brown in color *Hoffmannihadrurus gertschi* (Soleglad, 1976)
- : External accessory trichobothria absent on chela; 16–19 (17.227) ventral trichobothria present on chela;

aculear glands present on telson in mature male; pedipalps, metasoma, and telson yellow in color *Hoffmannihadrurus aztecus* (Pocock, 1902)

3: 1–5 external accessory trichobothria present on chela (“*hirsutus*” group) **4**

■: External accessory trichobothria absent on chela (“*arizonensis*” group) **6**

4: 1–2 external accessory trichobothria present on chela, none located on base of fixed finger; 3–5 (4.1) internal accessory trichobothria present on chela; 14–20 (17.5) ventral trichobothria on chela **5**

■: 3–5 external accessory trichobothria present on chela, one located on base of fixed finger; 5–7 (5.6) internal accessory trichobothria present on chela; 22–32 (25.6) ventral trichobothria on chela *Hadrurus pinteri* Stahnke, 1969

5: Aculear gland absent on telson in mature male; 14–16 (15.7) ventral trichobothria on chela; pectinal teeth 28–35 in males and 22–27 in females *Hadrurus hirsutus* (Wood, 1863)

■: Aculear gland present on telson in mature male; 15–20 (17.8) ventral trichobothria on chela; pectinal teeth 34–40 in males and 27–33 in females *Hadrurus concolorous* Stahnke, 1969

6: 4–7 (5.5) internal accessory trichobothria on chela; 15–22 (19.0) ventral trichobothria on chela; metasomal ventromedian intercarinal area lacking setae; chelal fingers yellow in color not contrasting with palm (“*arizonensis*” subgroup) **7**

■: 2–4 (2.4) internal accessory trichobothria on chela; 13–17 (15.0) ventral trichobothria on chela; metasomal ventromedian intercarinal area with irregularly positioned setae; chelal fingers reddish-orange in color contrasting with palm (“*spadix*” subgroup) **8**

7: Dorsal carinae of metasoma segment III with setae; 4–7 (5.5) internal accessory trichobothria on chela; 16–22 (19.1) ventral trichobothria on chela *Hadrurus arizonensis arizonensis* Ewing, 1928

■: Dorsal carinae of metasoma segment III lacking setae; 4–5 (4.8) internal accessory trichobothria on chela; 15–20 (18.1) ventral trichobothria on chela *Hadrurus arizonensis austrinus* Williams, 1970

8: 2–3 (2.1) internal accessory trichobothria on chela; carapace interocular area variable, completely melanic or with irregular shallow crescent-shaped clear pattern extending from lateral eyes towards but not reaching the median eyes **9**

■: 2–4 (3.0) internal accessory trichobothria on chela; carapace interocular area with distinct V-shaped clear

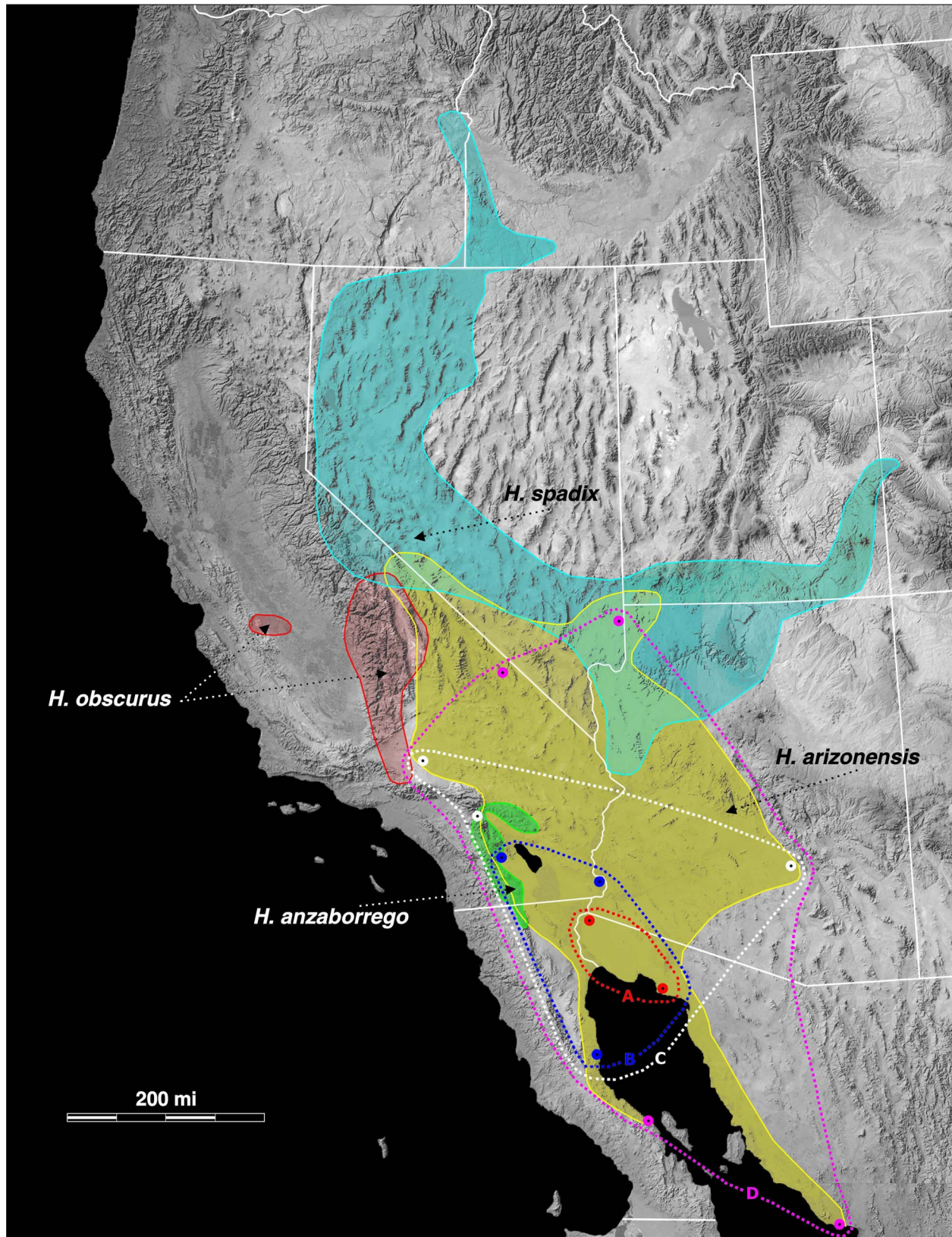


Figure 2: Reported distribution of *Hadrurus* “*arizonensis*” group. Distribution based primarily on Williams (1970, 1980), Fet & Soleglad (2008), and new locality data reported in this study for *H. obscurus*. Concentric polygons represent numbers of accessory trichobothria (decreasing from A to D) in *H. arizonensis*, see Table 1 for details.

	Internal Accessory	Ventral *
<i>H. arizonensis arizonensis</i>		
Puerto Peñasco, Sonora, Mexico - A	5–7 (6.091) [022]	18–22 (19.909) [022]
San Luis, Sonora, Mexico - A	5–6 (5.833) [024]	18–22 (19.826) [023]
San Diego Co. (ABDSP), California, USA - B	5–7 (5.714) [035]	17–22 (19.139) [036]
Imperial Co. (Picacho), California, USA - B	5–6 (5.706) [017]	16–22 (19.471) [017]
Puertocitos, Baja California, Mexico - B	5–6 (5.571) [021]	18–21 (19.476) [021]
Maricopa Co. (E. Mesa), Arizona, USA - C	4–6 (5.527) [074]	16–22 (19.026) [076]
Los Angeles & Riverside Co., California, USA - C	5–6 (5.235) [017]	17–20 (18.188) [016]
Clark Co. (Mesquite Valley), Nevada, USA ** - D	5–6 (5.083) [012]	17–20 (18.500) [012]
Inyo Co., California, USA - D	5–5 (5.000) [008]	17–20 (18.125) [008]
Southern (Guaymas) Sonora, Mexico - D	4–5 (4.875) [016]	16–19 (17.625) [016]
<i>H. arizonensis austrinus</i>		
Oakies Landing, Baja California, Mexico - D	4–5 (4.769) [026]	15–20 (18.083) [024]
“arizonensis” subgroup Total	4–7 (5.474) (± 0.594) [274] (4.880–6.068)	15–22 (18.978) (± 1.234) [273] (17.75–20.21)
“spadix” subgroup Total	2–4 (2.399) (± 0.513) [268] (1.886–2.912)	13–17 (14.898) (± 0.846) [235] (14.05–15.74)
Statistical comparisons between subgroups (internal / ventral): *** MVD = 128.18 / 27.39 % SERS = 191.81 / 118.93 % ANOVA <i>p</i> -value = 1E-255/ 3.5E-170		

Table 1: Chelal neobothriotaxy statistical comparisons for the *Hadrurus* “arizonensis” and “spadix” subgroups. Localities for “arizonensis” subgroup are ordered from largest to smallest numbers as indicated by the internal accessory trichobothria (see map in Fig. 2 where four concentric polygons illustrate these localities, identified as A–D). Statistical data group = minimum–maximum (mean) (\pm standard error) [N] (standard error range). * includes orthobothriotaxic trichobothria V_1 – V_4 . ** data courtesy of Mathew R. Graham. *** Mean Value Difference, Standard Error Range Separation, Analysis of Variance.

pattern extending from lateral eyes to the median eyes...
Hadrurus anzaborrego Soleglad, Fet et Lowe, **sp. nov.**

- 9: Carapace completely melanic.....
.....*Hadrurus spadix* Stahnke, 1940
■: Carapace interocular area with irregular shallow
crescent-shaped clear pattern extending from lateral eyes
towards but not reaching the median eyes
.....*Hadrurus obscurus* Williams, 1970

Hoffmannihadrurus

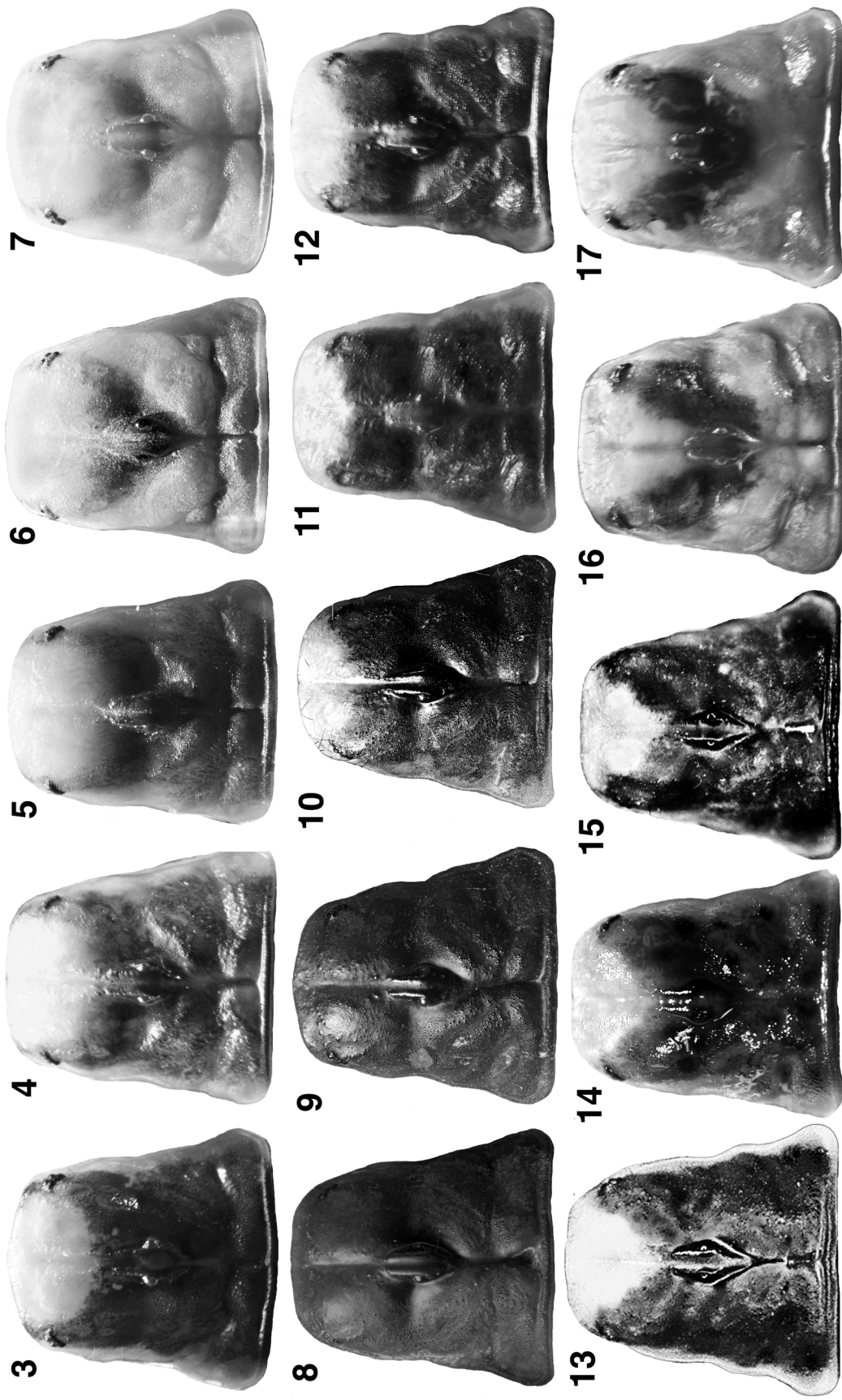
Hoffmannihadrurus is comprised of two species, both distributed in southern mainland Mexico. *H. aztecus* has been reported from the states of Oaxaca, Puebla, and Veracruz (questionable?). *H. gertschi* has only been reported from the state of Guerrero. In addition to the important six diagnostic characters stated in the key above, species of this genus also can be separated from its northern sister genus *Hadrurus* by the absence of the paired median carinae on sternite VII,

lesser setation of the pedipalp patella internal surface and dorsal aspects of metasomal segments IV–V, and by the distinct reddish pigmented ventral carinae of the metasoma.

Hadrurus

As shown in the phylogenetic key, *Hadrurus* is divided into two groups, the “hirsutus” group, exclusively found in the Baja California peninsula, and the “arizonensis” group, occurring in the southwestern United States and northern Baja California and Sonora, Mexico. These two groups, plus the genus *Hoffmannihadrurus*, comprise the three original phylogeographic partitions of *Hadrurus* suggested by Williams (1970: 31–32).

The “hirsutus” group of *Hadrurus* is comprised of three species, *H. pinteri*, occurring in the central-east portion of the Baja California peninsula in primarily volcanic areas, *H. concolorous*, occurring throughout most of central and southern Baja California, and *H.*



Figures 3–17: Carapace pattern schemes for the *Hadrurus "arizonensis"* group. **3.** *H. arizonensis arizonensis*, juvenile male, typical dark phenotype, Rte 178, 0.5 W Rte 127, Inyo Co., California, USA. **4.** *H. a. arizonensis*, male, variegated phenotype, Tecopa Hot Springs, Old Spanish Trail, Inyo Co., California, USA. **5.** *H. a. arizonensis*, male, variegated phenotype, Rocky Buttes, Antelope Valley, Los Angeles Co., California, USA. **6.** *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. **7.** *H. arizonensis austrinus*, subadult female, Oakies Landing, Baja California, Mexico. **8.** *H. spadix*, female, Towne Pass, Panamint Range, Inyo Co., California, USA. **9.** *H. obscurus*, female, Bird Spring Canyon Road, Kern Co., California, USA. **10.** *H. obscurus*, male, Bird Spring Canyon Road, Kern Co., California, USA. **11.** *H. obscurus*, male, Jawbone Canyon Road, Kern Co., California, USA. **12.** *H. obscurus*, male, Palmdale, Los Angeles Co., California, USA. **13.** *H. anzaborrego* (dark phenotype), male, Borrego Springs, San Diego Co., California, USA. **14.** *H. anzaborrego* (dark phenotype), male, Yaqui Pass, ABDSP, San Diego Co., California, USA. **15.** *H. anzaborrego* (dark phenotype), male, Borrego Springs, San Diego Co., California, USA. **16.** *H. anzaborrego* (pale phenotype), female, Indian Gorge Canyon, ABDSP, San Diego Co., California, USA. **17.** *H. anzaborrego* (pale phenotype), male, Pinyon Mountain Road, ABDSP, San Diego Co., California, USA.

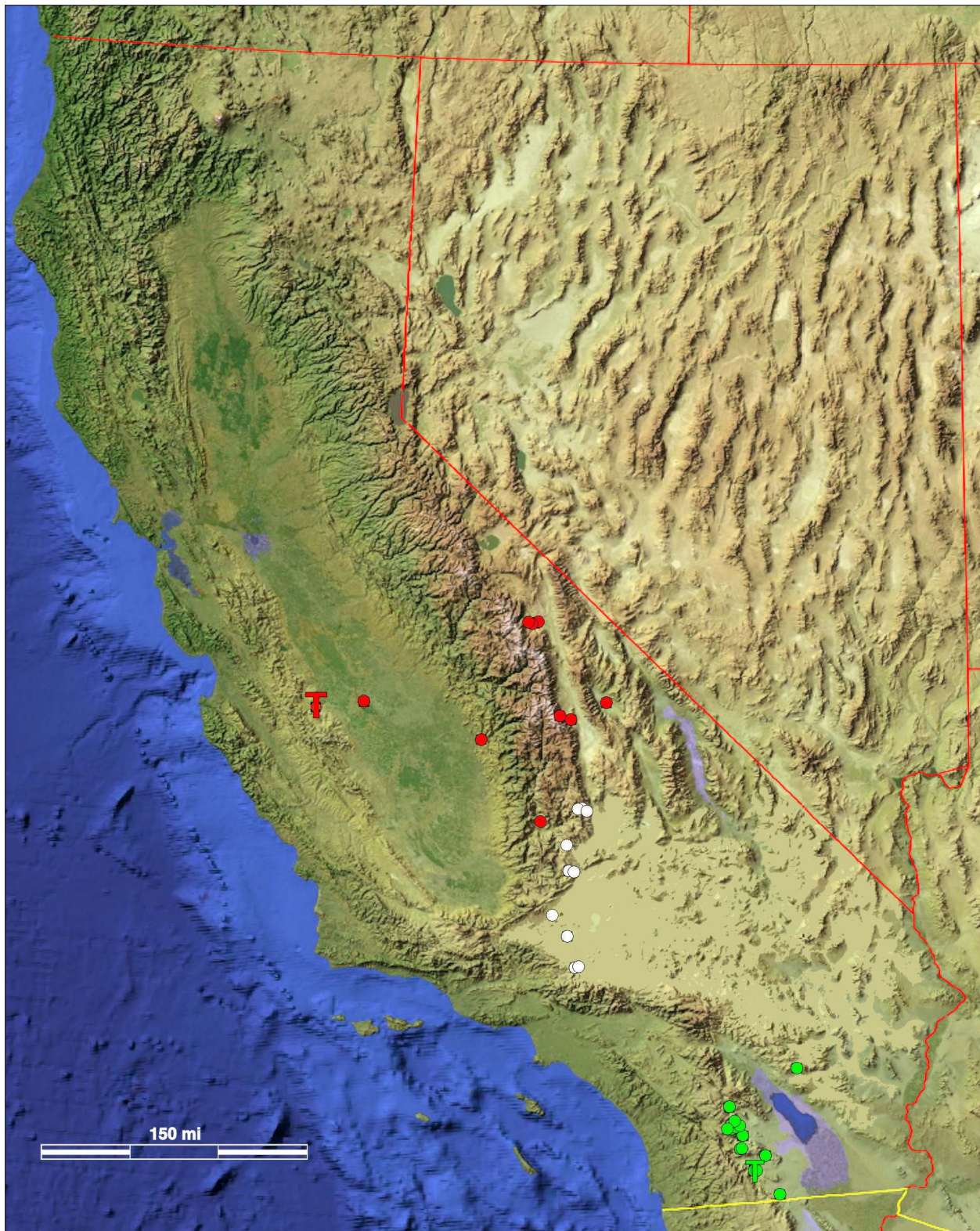


Figure 18: Distribution of three primary populations of *Hadrurus obscurus* and *H. anzaborrego*, **sp. nov.**, reported in literature and/or examined in this study. The northern population, the original Williams' (1970) records of *Hadrurus obscurus*, including type locality (red T), are indicated with red icons. The central population, white icons, are localities of *Hadrurus obscurus* examined in this study. The southern population, *H. anzaborrego*, **sp. nov.**, primarily from the Anza-Borrego Desert State Park (ABDSP), are indicated with green icons (type locality marked with green T).

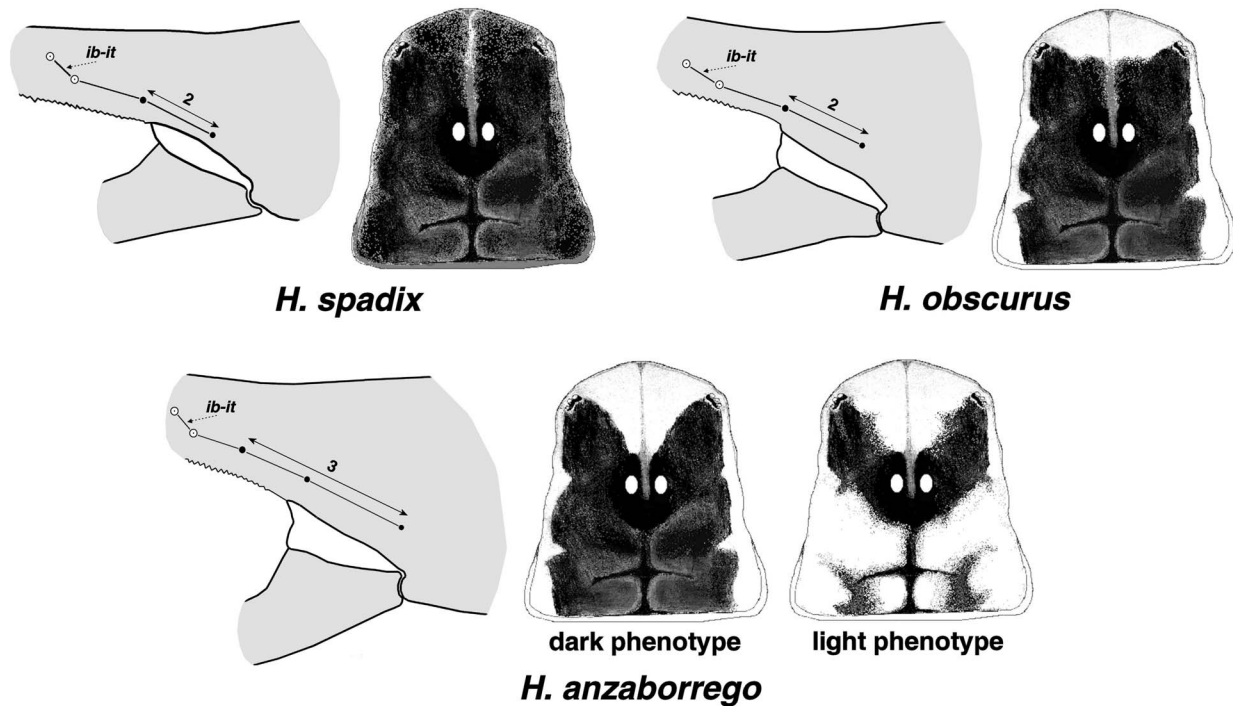


Figure 19: Diagnostic characters separating the three species of the *Hadrurus* “*spadix*” subgroup. Note that *H. spadix* and *H. obscurus* have two internal accessory trichobothria (dark circles) placed essentially in the same locations, whereas *H. anzaborrego* has three which are configured differently. Refer to statistical data supporting these two patterns in Fig. 21. The carapacial patterns are different in all three species, with species *H. anzaborrego* exhibiting two color phenotypes. Carapace patterns from Fet, Soleglad & Barker (2001), in part.

hirsutus restricted to the extreme southern “cape region” of Baja California.

The “*arizonensis*” group is comprised of two subgroups, the “*arizonensis*” subgroup and “*spadix*” subgroup, spanning four species and one subspecies, including new species *H. anzaborrego* described in this contribution. The “*arizonensis*” subgroup is comprised of one species *Hadrurus arizonensis*, which is divided into two subspecies. *H. arizonensis arizonensis* is found in southern California, west central Arizona, southern Nevada, northern Baja California, and northwestern Sonora, Mexico, and *H. arizonensis austrinus* found only in an isolated east coastal volcanic area in central Baja California. Three species are placed in the “*spadix*” subgroup: *H. spadix* is distributed in northern Arizona, western Nevada, east-central edge of California, and southern portions of Utah and Idaho; *H. obscurus* is found in central California extending to its border with Nevada; and *H. anzaborrego* is distributed in the extreme south central area of California, restricted to the Colorado Desert.

Hadrurus “*arizonensis*” and “*spadix*” subgroups

As indicated in the key above, the “*arizonensis*” and “*spadix*” subgroups of *Hadrurus* can be diagnosed by

several characters involving accessory trichobothria numbers and their relative positions, coloration, and setation.

Table 1 presents a set of statistics of trichobothria numbers based on over 250 specimens examined from these two *Hadrurus* subgroups. There is noticeable variability in numbers of accessory trichobothria in the “*arizonensis*” subgroup; this variability is not random, however, but can be correlated to specific geographic regions. Therefore, in Table 1 the data for this subgroup are partitioned into several geographic localities throughout southern United States, Baja California, and mainland Mexico. In the map shown in Fig. 2, these localities are contained in concentric polygons representing decreasing accessory trichobothria numbers from the center polygon outwards. The largest numbers of accessory trichobothria are found in populations from northern Sonora, Mexico (polygon A). From this “central region” we see an increased reduction in neobothriotaxy from localities contained in outside polygons as follows, the outermost polygon representing regions with the lowest number of accessory trichobothria: polygon A includes northern Sonora, Mexico (San Luis and Puerto Peñasco); polygon B includes regions in the Colorado Desert from southern California and Arizona (ABDSP and Picacho), to central



Figure 20: Carapace patterns of *Hadrurus obscurus* showing both dark (left, a female, carapace length = 8.87 mm) and pale (right, a male, carapace length = 12.04 mm) phenotypes from same locality. Bird Spring Canyon Road, Kern Co., California, USA. See Figs. 3–17 for comparison of all “*arizonensis*” group carapace patterns.

Baja California (Puertocitos); polygon C includes regions from central Arizona (Mesa), and the southern portion of the Mojave Desert (Riverside and Los Angeles Counties); polygon D includes the outer distributions of the “*arizonensis*” subgroup, exhibiting the lowest numbers of accessory trichobothria, northern Mojave Desert (Inyo County and the Arizona-Nevada region), west-central Sonora, Mexico (Guaymas), and the southwestern Baja California volcanic region (Oakies Landing, subspecies *H. arizonensis austrinus*). Regardless of the lower accessory trichobothria numbers as found in populations from the outer edges of proposed *H. arizonensis* radiation (see “accessory trichobothria loss hypothesis” by Fet & Soleglad (2008)), the “*spadix*” subgroup trichobothria numbers are considerably less than these lowest numbers, averaging 2.4 and 2.7 less accessory trichobothria in the internal and ventral series, respectively. Comparing the *average* numbers across the two subgroups, the “*spadix*” subgroup exhibits 3 less internal and 4 less ventral accessory trichobothria than the “*arizonensis*” subgroup.

Soleglad (1976) pointed out a difference in the relative position of chelal trichobothrium *Est* between these two subgroups (see Soleglad, 1976: fig. 1, for method of measurement). In the “*arizonensis*” subgroup, *Est* is positioned roughly midpoint on the chelal palm, in a ratio of 0.45–0.53 (0.486) [113] whereas its position in the “*spadix*” subgroup is more distal on the palm, in a

ratio of 0.36–0.46 (0.409) [72] (note, the specified ranges are standard error ranges). The MVD and *p*-value of this ratio is 18.8 % and 3.34E-24 (ANOVA) based on 185 samples. It must be stressed, however, that although statistically this ratio is significant, there exists some positional dislocation of this trichobothrium on individual specimens, and therefore a consensus must be tabulated from both chelae and multiple specimens from any given population.

As originally pointed out by Williams (1970), both *H. spadix* and *H. obscurus* have numerous setae occurring between the ventromedian carinae of metasomal segments I–III (see Figs. 31–33). As stated in its description below, new species *H. anzaborrego* also has setae in these intercarinal areas of the metasoma (see Fig. 47). In contrast, the two subspecies of *H. arizonensis* in general lack setae between the ventromedian carinae of the metasoma.

We can differentiate the two subgroups based on the multitude of carapacial patterns. In both subspecies of *H. arizonensis*, a distinct crescent-shape melanic pattern is present on the anterior half of the carapace, interconnecting the lateral and median eyes. However, the area posterior to the interocular area is variable: clear in some phenotypes, completely melanic to variegated in pattern in others. See Figs. 3–7 for examples of these patterns. Three distinct patterns are found in the three species of the “*spadix*” group. Completely melanic with-

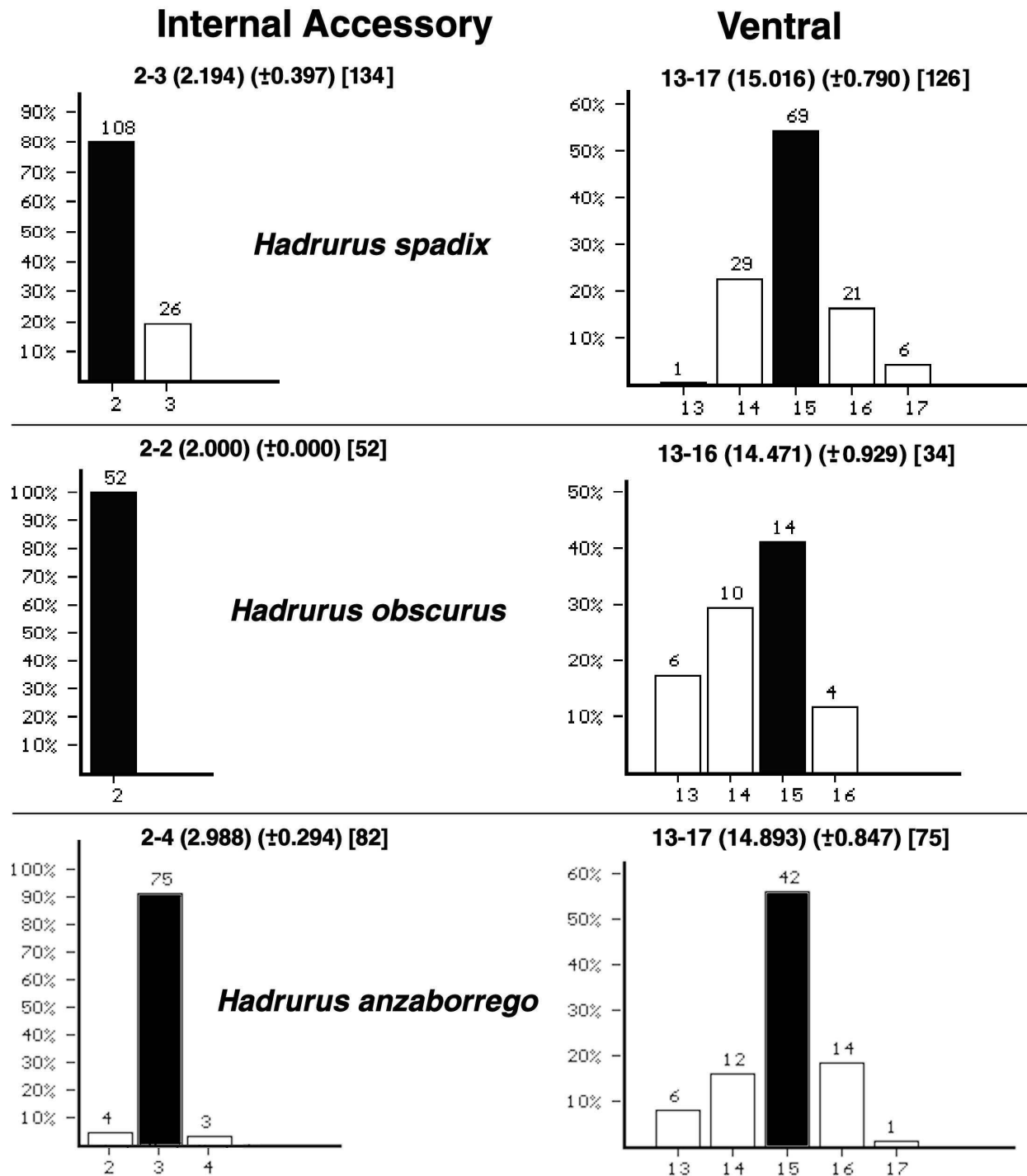
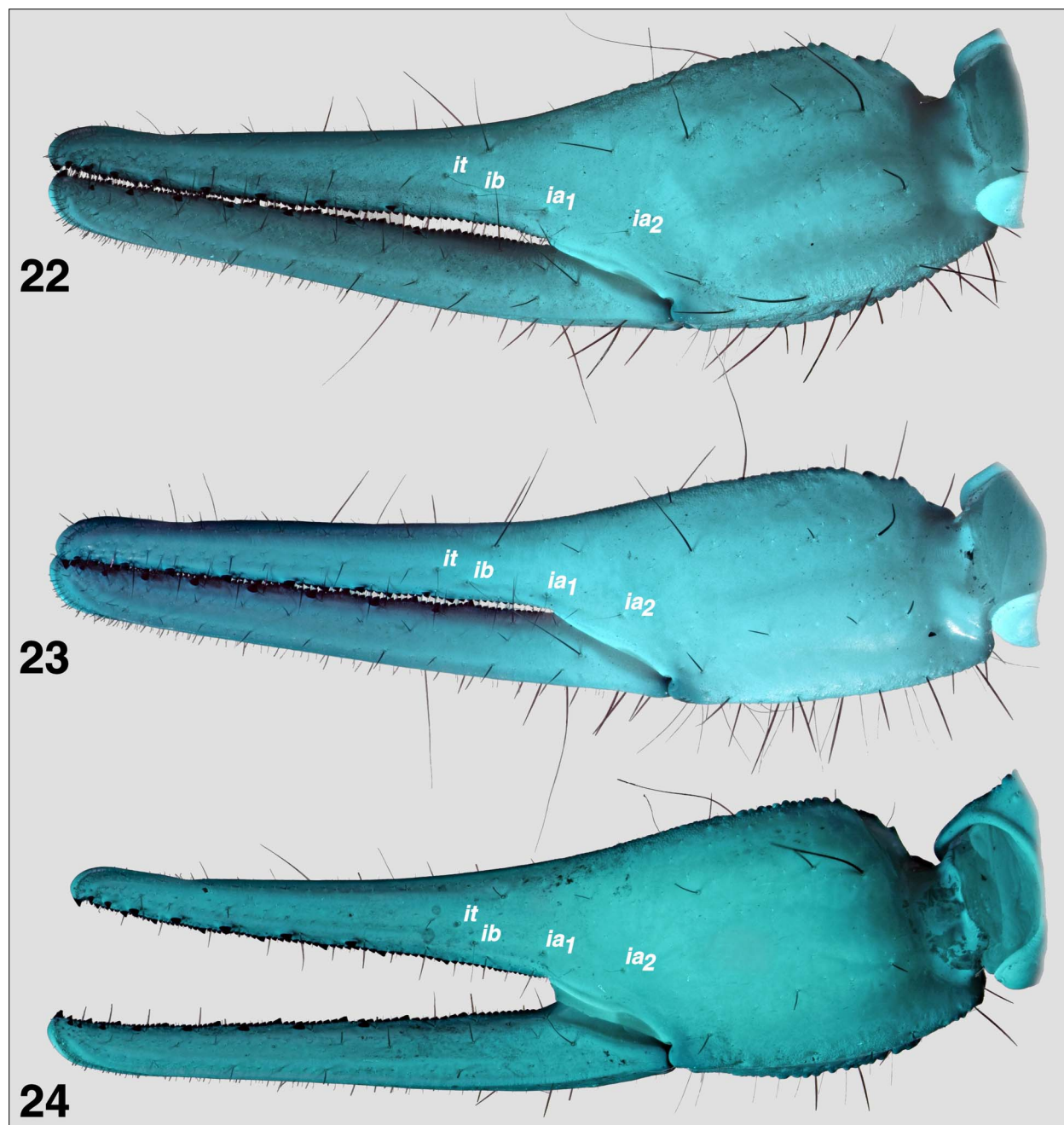


Figure 21: Chelal trichobothria statistics for the *Hadrurus* “spadix” subgroup. The data shows that *Hadrurus anzaborrego*, **sp. nov.**, exhibits three internal accessory trichobothria, supported by over 90 % of the samples, whereas *H. obscurus* and *H. spadix* have two accessory internal trichobothria, as supported by 86 % of the data. See Fig. 19 for examples of these patterns. Portion of *H. obscurus* data courtesy of Mathew R. Graham. Note that the ventral trichobothria data, which are essentially the same across all three species, include the orthobothriotaxic V_1 – V_4 .

out variegation in *H. spadix* (Fig. 8), a shallow clear oval in the interocular area anterior of the median eyes in *H. obscurus* (Figs. 10–12) and a distinct wedge-shaped clear area extending from the anterior edge to the

median eyes in *H. anzaborrego* (Figs. 13–17). [It is important to note here, however, that a dark phenotype of *H. obscurus* (Fig. 9) was examined in this study, exhibiting a carapace pattern as seen in *H. spadix*, see



Figures 22–24: Comparisons of *Hadrurus obscurus* and *H. spadix*, chelal internal trichobothria, showing *two* accessory trichobothria. **22.** *H. obscurus*, male (pale phenotype, chela length = 17.65 mm), Bird Spring Canyon Road, Kern Co., California, USA. **23.** *H. obscurus*, female (dark phenotype, chela length = 12.85 mm), Bird Spring Canyon Road, Kern Co., California, USA. **24.** *H. spadix*, female (chela length = 19.38 mm), Towne Pass, Panamint Range, Inyo Co., California, USA.

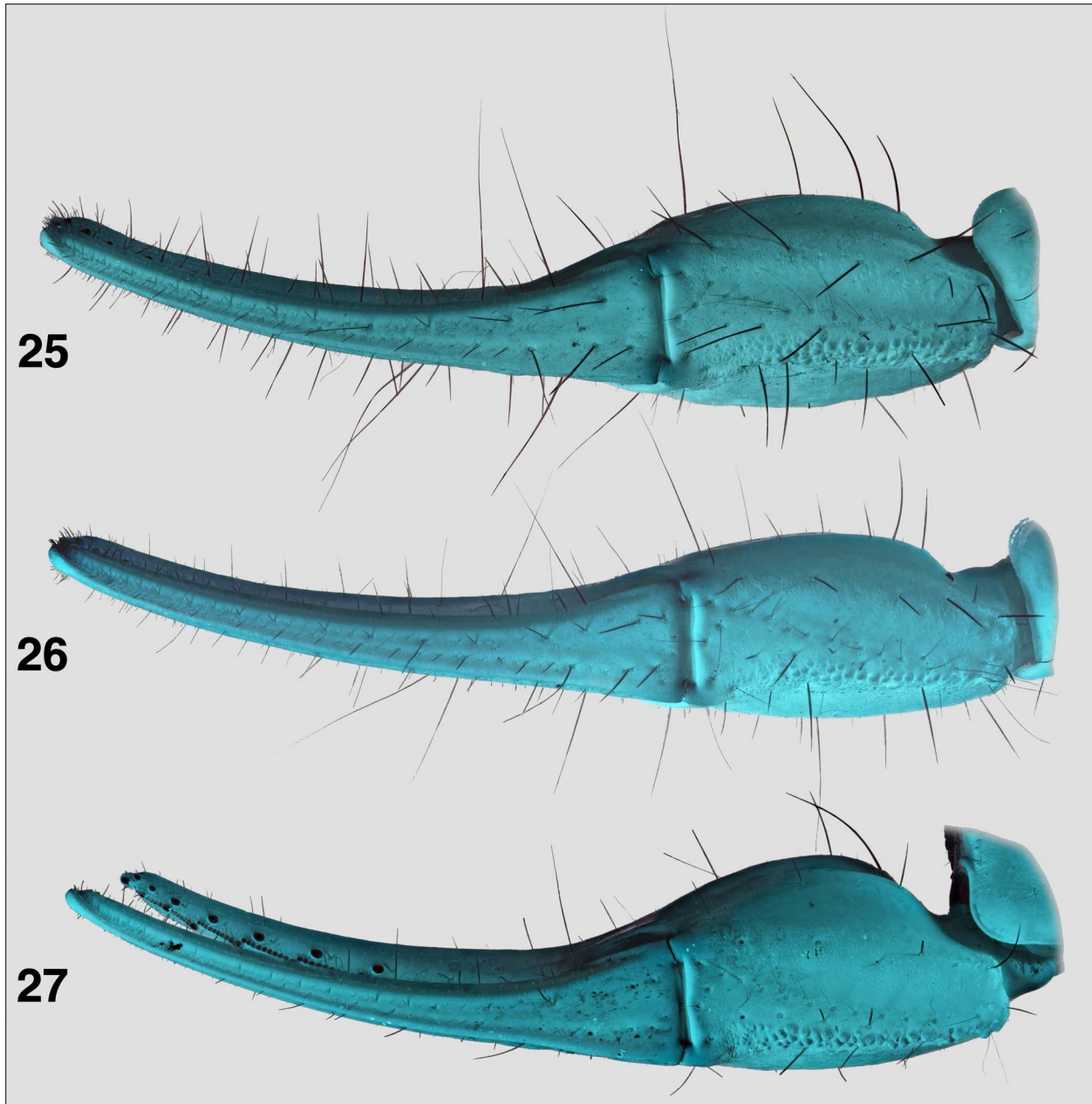
below for further information.] In *H. anzaborrego*, two color-based phenotypes are present, a dark form where the posterior half of the carapace and mesosoma is melanitic, and a pale form where the wedge-shaped melanitic pattern is restricted to the interocular area and mesosoma is more yellow in color.

All three species of the “*spadix*” subgroup have pigmented chelal fingers, contrasting with the yellow

palm (although this pigmentation can be difficult to detect in some preserved specimens). In the “*arizonensis*” subgroup, the fingers are not pigmented.

Species in *Hadrurus* “*spadix*” subgroup

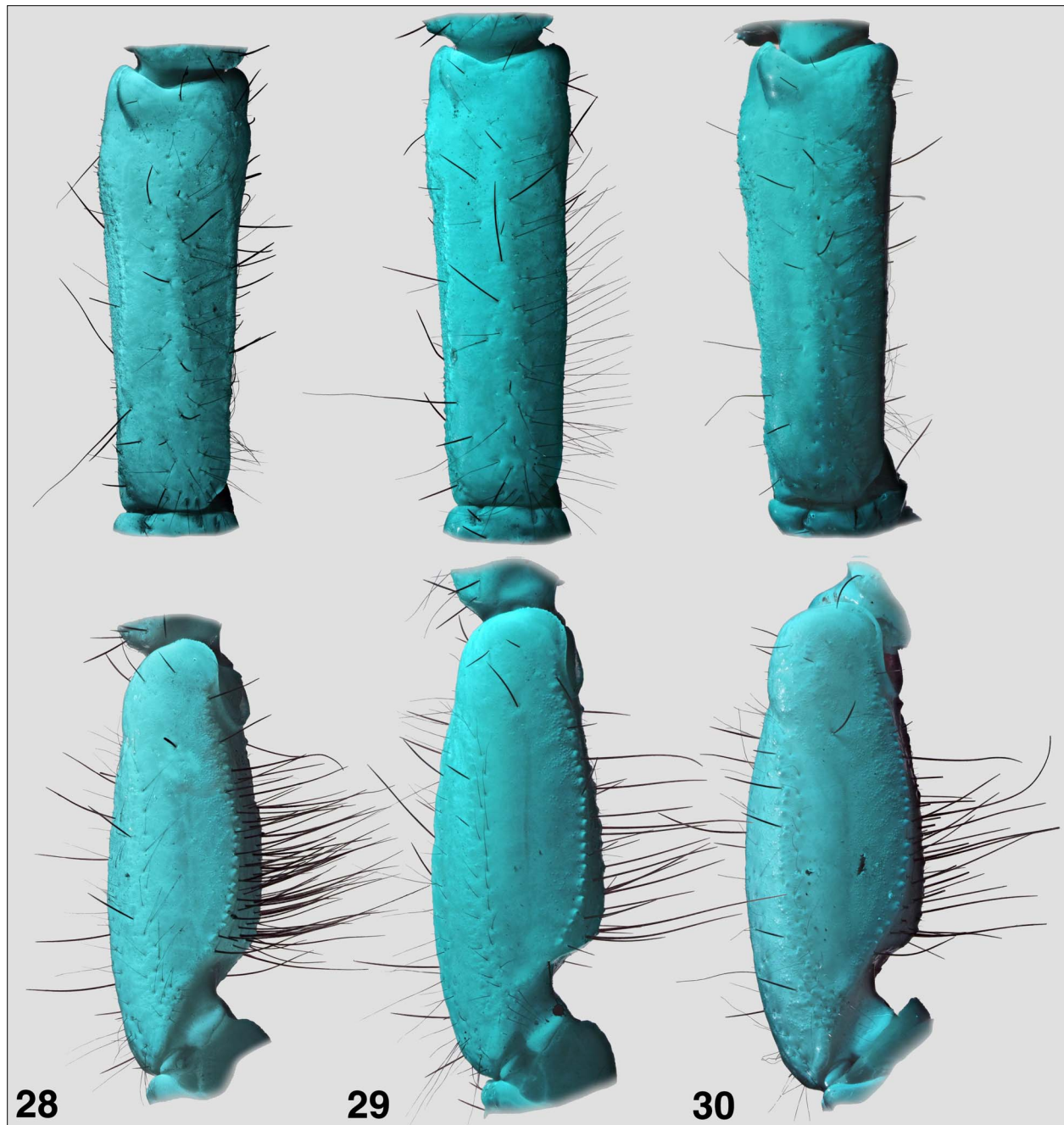
We have observed specimens of *H. obscurus* from Kern and Los Angeles Counties, which occur roughly



Figures 25–27: Comparisons of *Hadrurus obscurus* and *H. spadix*, chelal ventral trichobothria (counts [xx] indicated below).
 25. *H. obscurus*, male (pale phenotype, chela length = 17.65 mm) [15], Bird Spring Canyon Road, Kern Co., California, USA.
 26. *H. obscurus*, female (dark phenotype, chela length = 12.85 mm) [15], Bird Spring Canyon Road, Kern Co., California, USA.
 27. *H. spadix*, female (chela length = 19.38 mm) [14], Towne Pass, Panamint Range, Inyo Co., California, USA. Note, trichobothria counts exclude Et_1 , Et_2 , Est , and Eb_1 if visible.

mid-point between topotypic *H. obscurus* and *H. anzaborrego* (see map in Fig. 18). These specimens, in general, comply with the diagnostic characters of the central California type series specimens: two accessory trichobothria on the internal surface of the chela; carapace interocular clear between the lateral eyes forming a shallow crescent area that does not extend to the median tubercle; setae found between the ventro-median carinae of metasomal segments I–IV (i.e., 4–15-

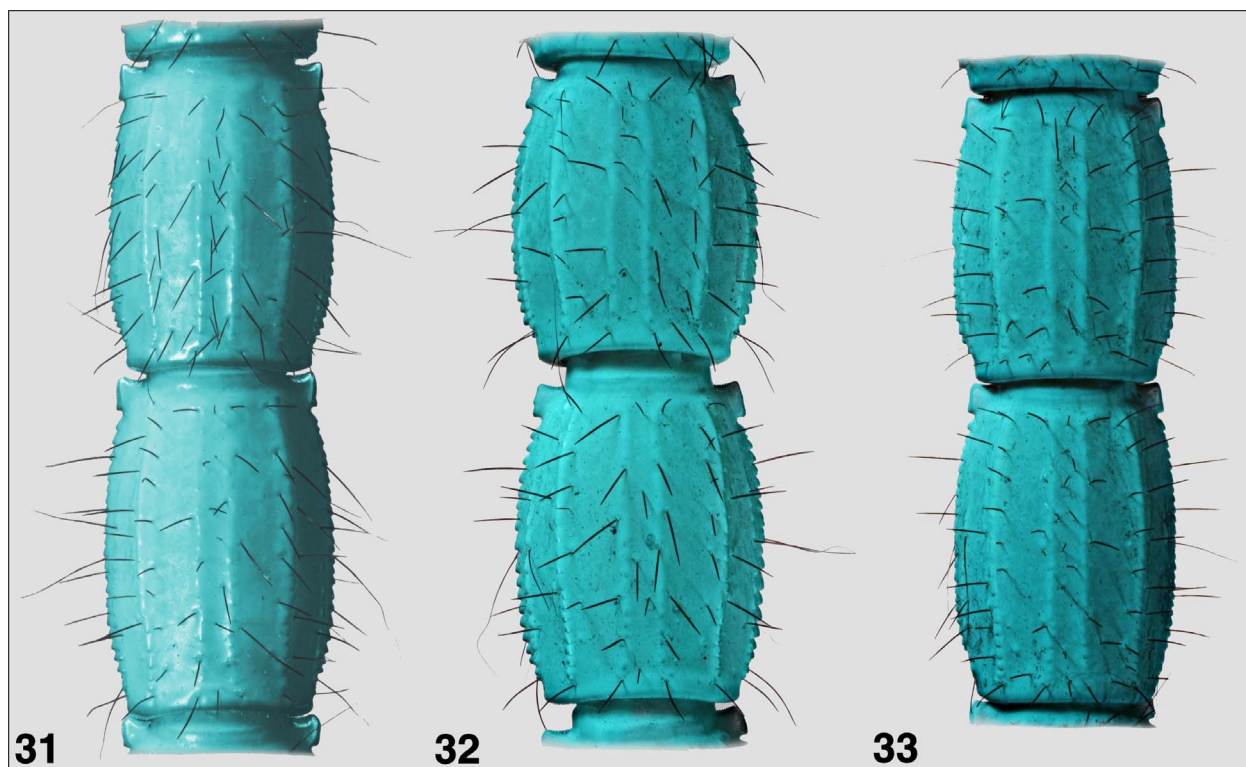
15–6 setae are found on a male specimen from Kern County); and chelal fingers reddish in color contrasting with the palm (note: this appears to be very subtle or lacking in the Los Angeles County specimens). These specimens do not show any intermediate stages of the first two characters between the northern populations and *H. anzaborrego* (i.e., primary diagnostic characters for this species) thus supporting the validity of this new species.



Figures 28–30: Comparisons of *Hadrurus obscurus* and *H. spadix* patella trichobothria, external (top) and ventral (bottom) views (counts [xx, xx] indicated below). **28.** *H. obscurus*, male (pale phenotype, patella length = 10.93 mm) [45, 28], Bird Spring Canyon Road, Kern Co., California, USA. **29.** *H. obscurus*, female (dark phenotype, patella length = 7.86 mm) [39, 29], Bird Spring Canyon Road, Kern Co., California, USA. **30.** *H. spadix*, female (patella length = 11.81 mm) [48, 29], Towne Pass, Panamint Range, Inyo Co., California, USA.

Based on trichobothrial information on *H. obscurus* (27 specimens total), we suspect that this species is in fact identical with *H. spadix*. In all cases, these 27 specimens have two internal accessory trichobothria on the chela, consistent with a majority of *H. spadix* (80 %). However, as shown in the histogram in Figure 21, roughly 20 % of *H. spadix* samples did exhibit three

internal accessory trichobothria where a majority of these specimens were clustered geographically in the Coconino Co., Arizona, and San Juan and Grand Co., Utah areas, somewhat removed from the reported locality of *H. obscurus*. The only discernable difference between these two species is the coloration pattern of the carapace as described elsewhere in this paper (see Fig.



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 melanistic 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.

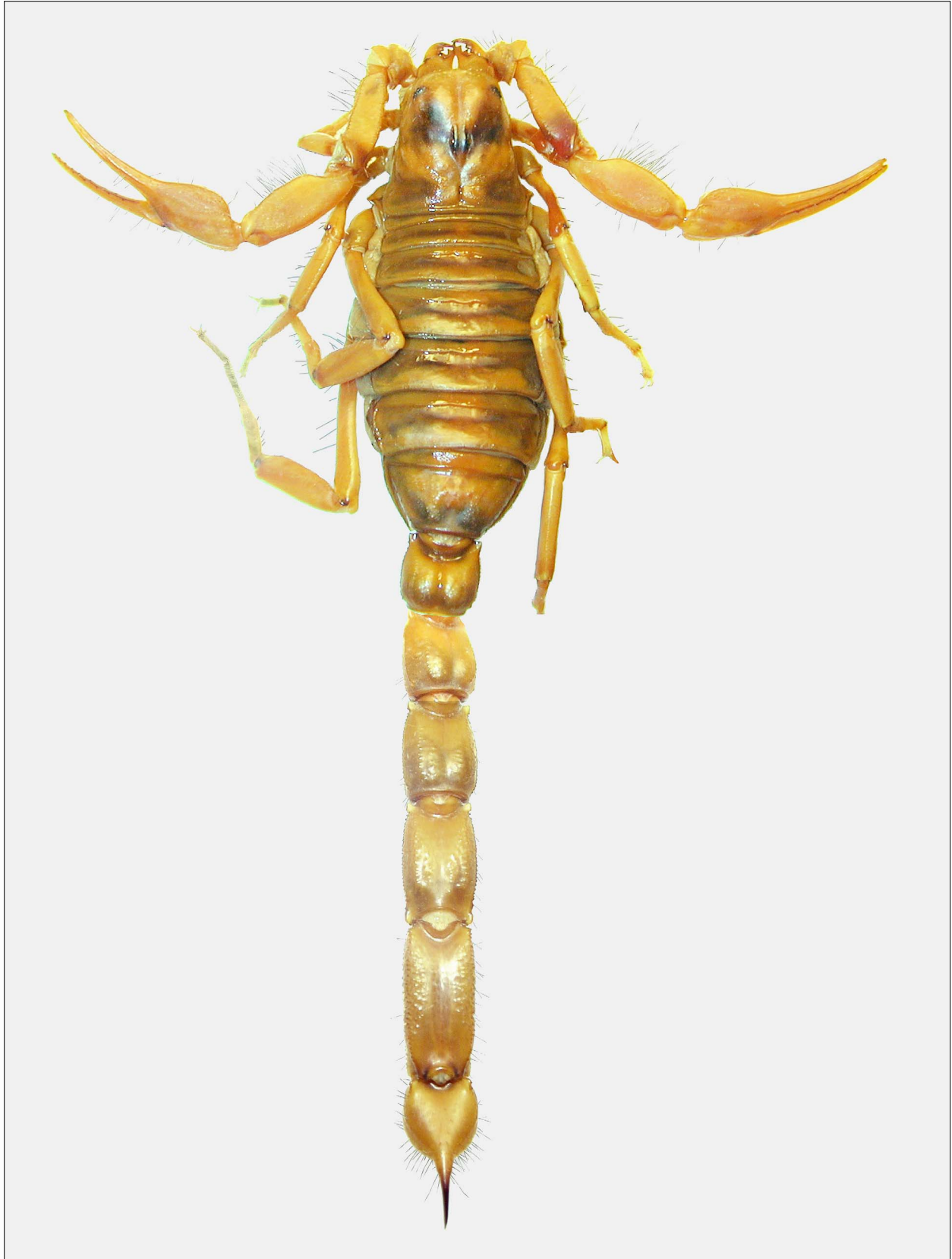
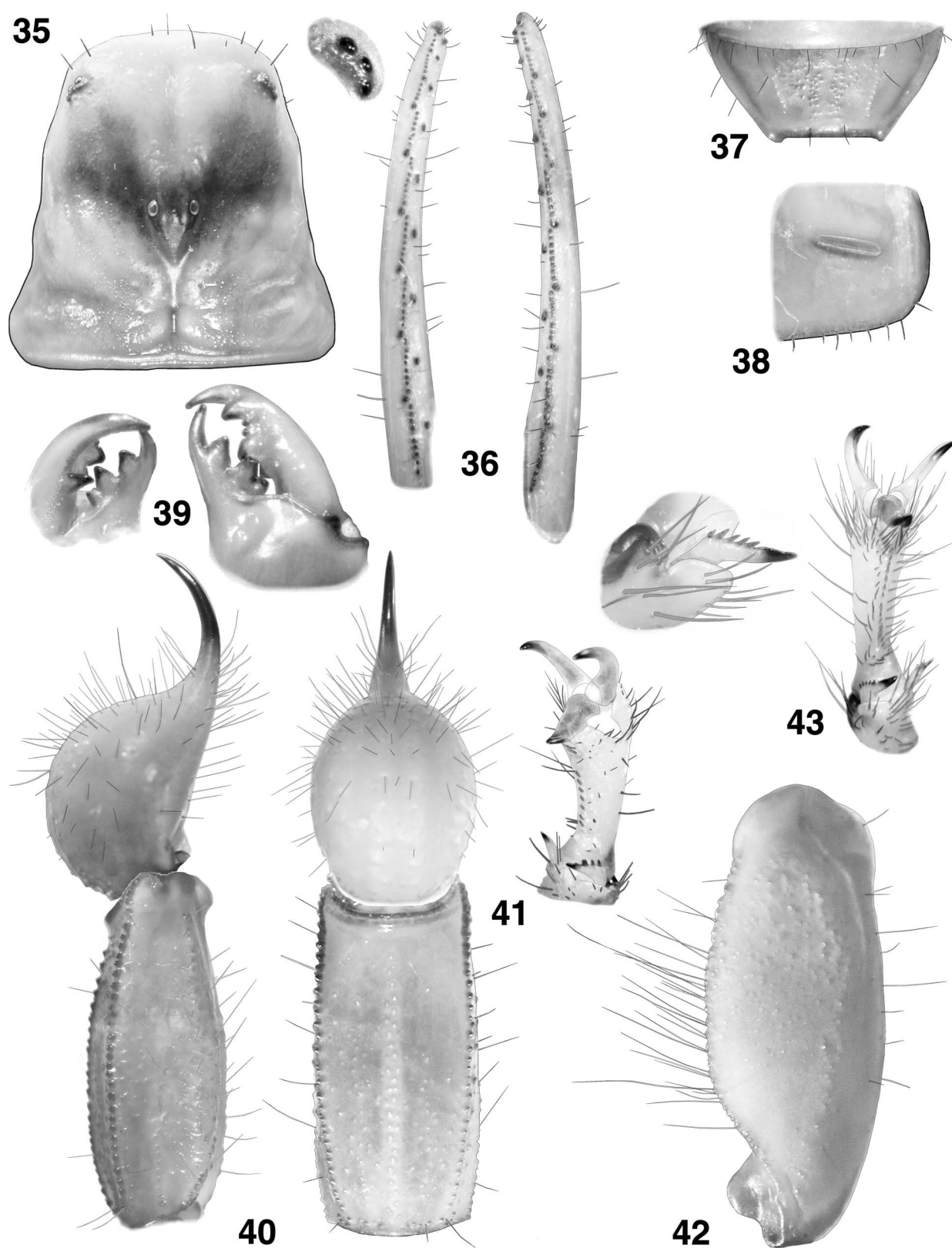


Figure 34: *Hadrurus anzaborrego*, sp. nov. Female holotype, Indian Gorge Canyon, ABDSP, California, USA. Dorsal view.



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 medium 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

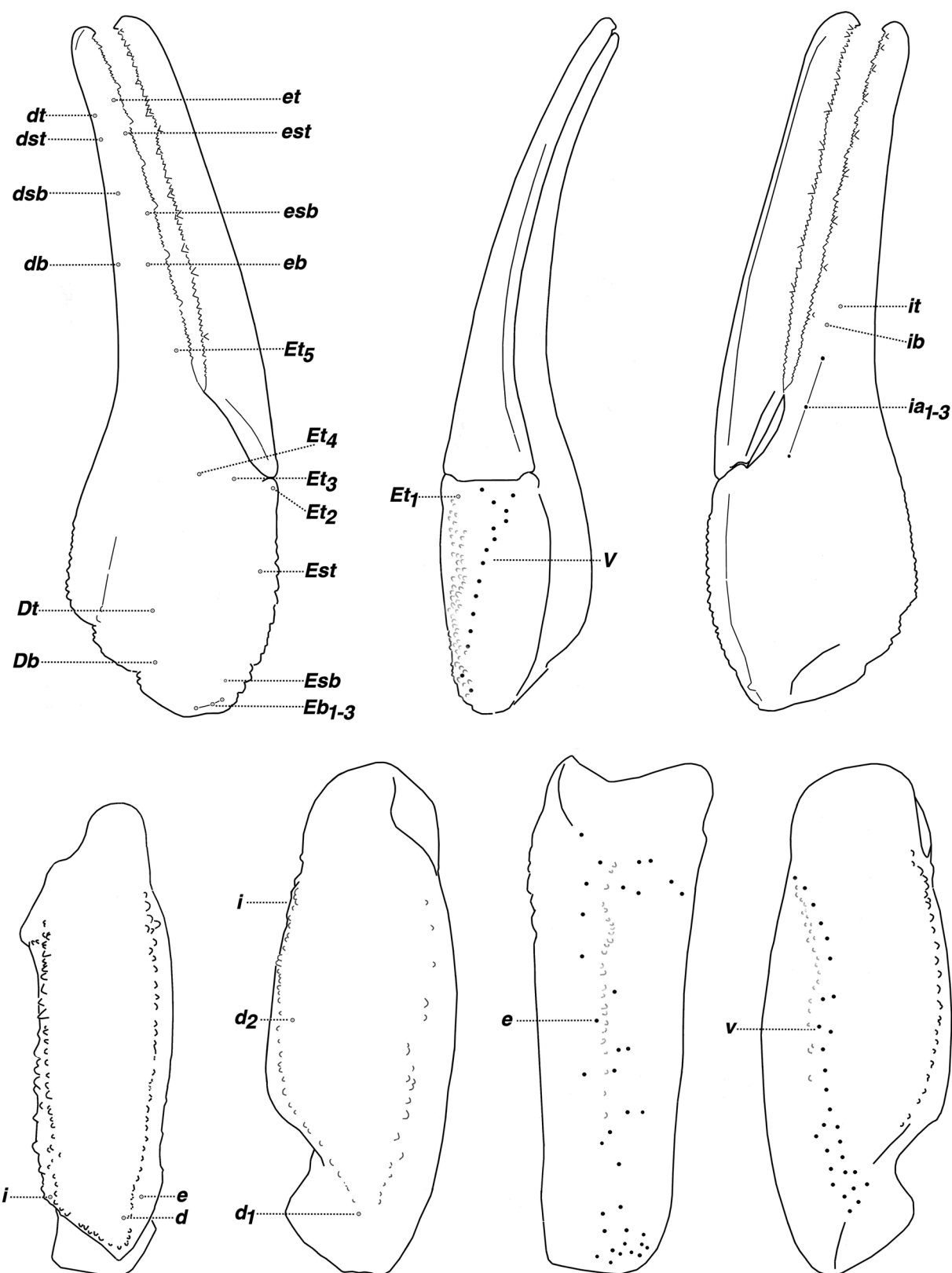
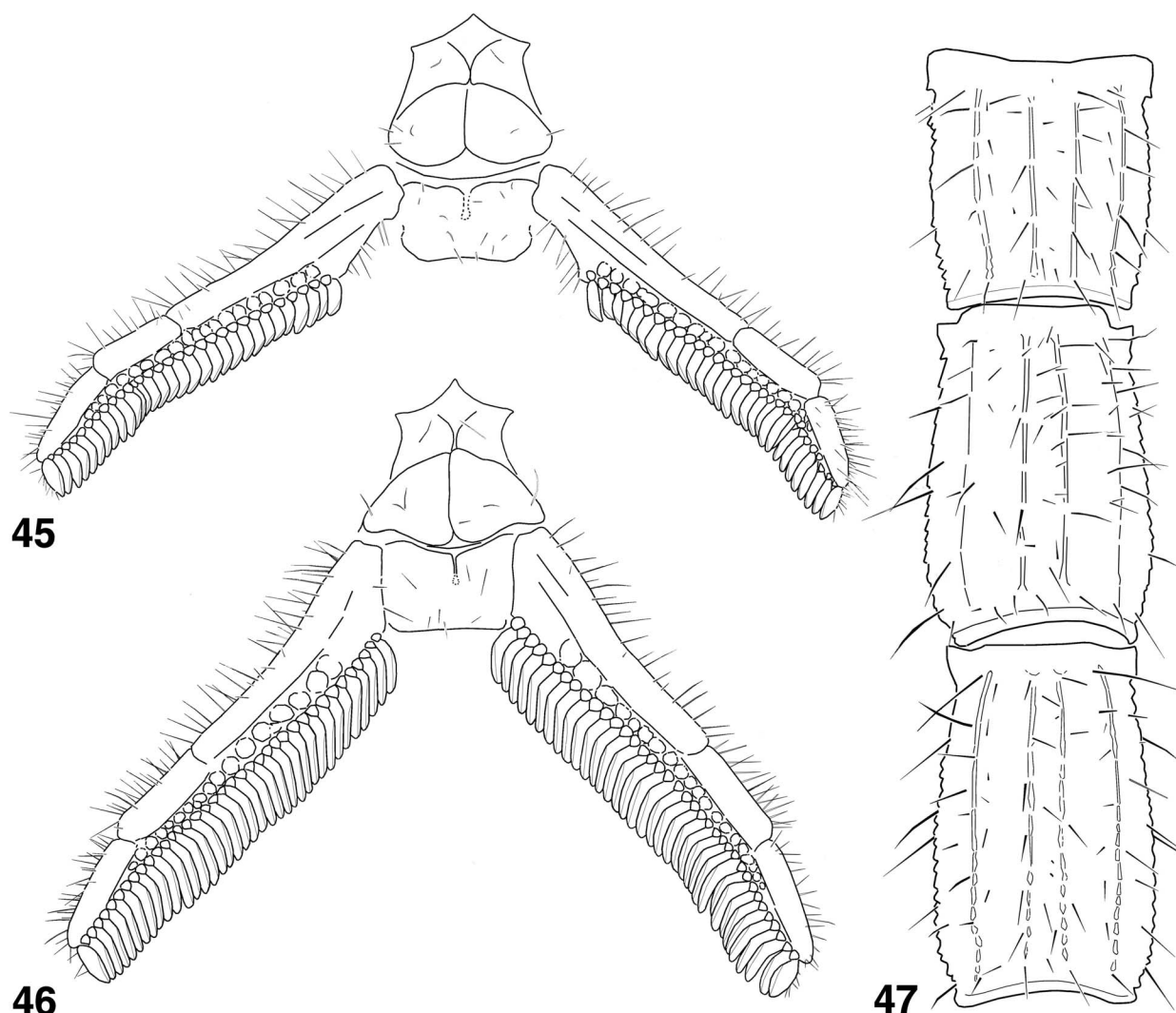


Figure 44: *Hadrurus anzaborrego*, sp. nov. Female holotype, Indian Gorge Canyon, ABDSP, California, USA. Trichobothrial pattern showing neobothriotaxy. Accessory trichobothria are indicated by closed circles. Note that chelal ventral and patellar ventral and external orthobothriotaxic trichobothria 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 *ID*s on fixed finger and 9/9 *ID*s on movable finger; 7/8 *OD*s on fixed finger and 9/9 *OD*s 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 anaborrego*, **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 anaborrego* 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) (± 1.836) [22] and the female 28–34 (30.400) (± 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) (± 3.171), II = 5–19 (10.652) (± 3.663), III = 3–13 (6.826) (± 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

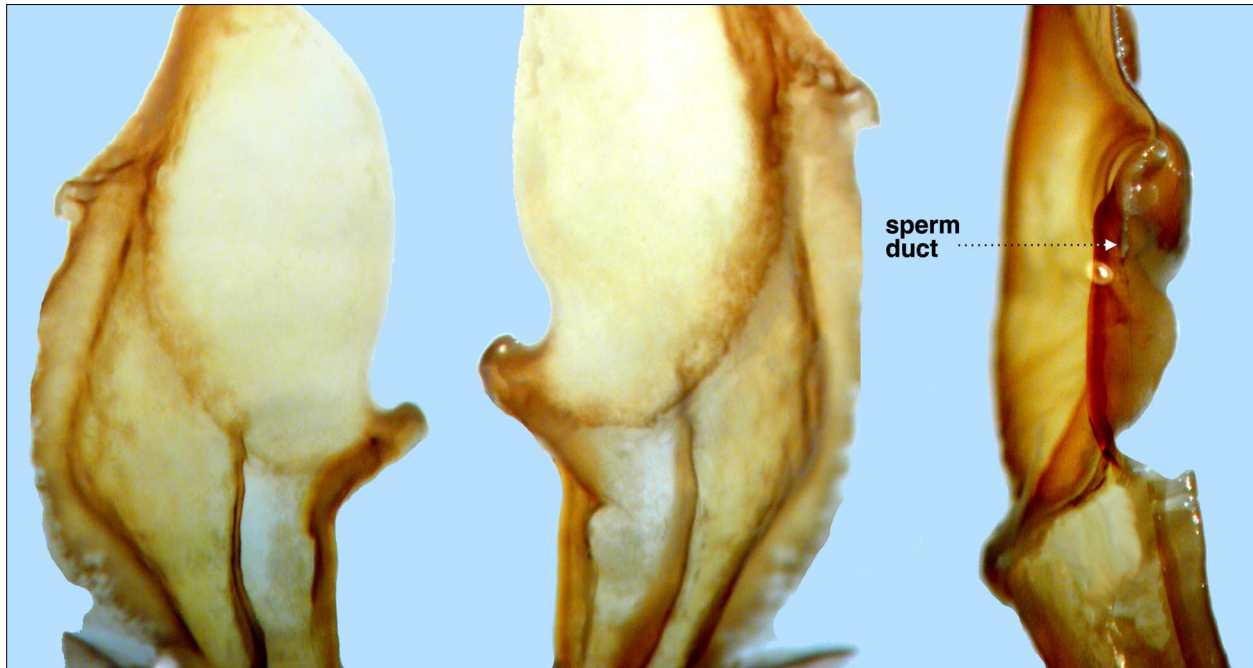


Figure 49: Close-up of median area of right hemispermatophore submerged in alcohol, dorsal, ventral, and internal (further magnified) views. *Sperm duct* indicated (after Stockwell, 1989: fig. 215). *Hadrurus anzaborrego*, **sp. nov.** (paratype male, light phenotypic), Pinyon Mountain, ABDSP, California,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

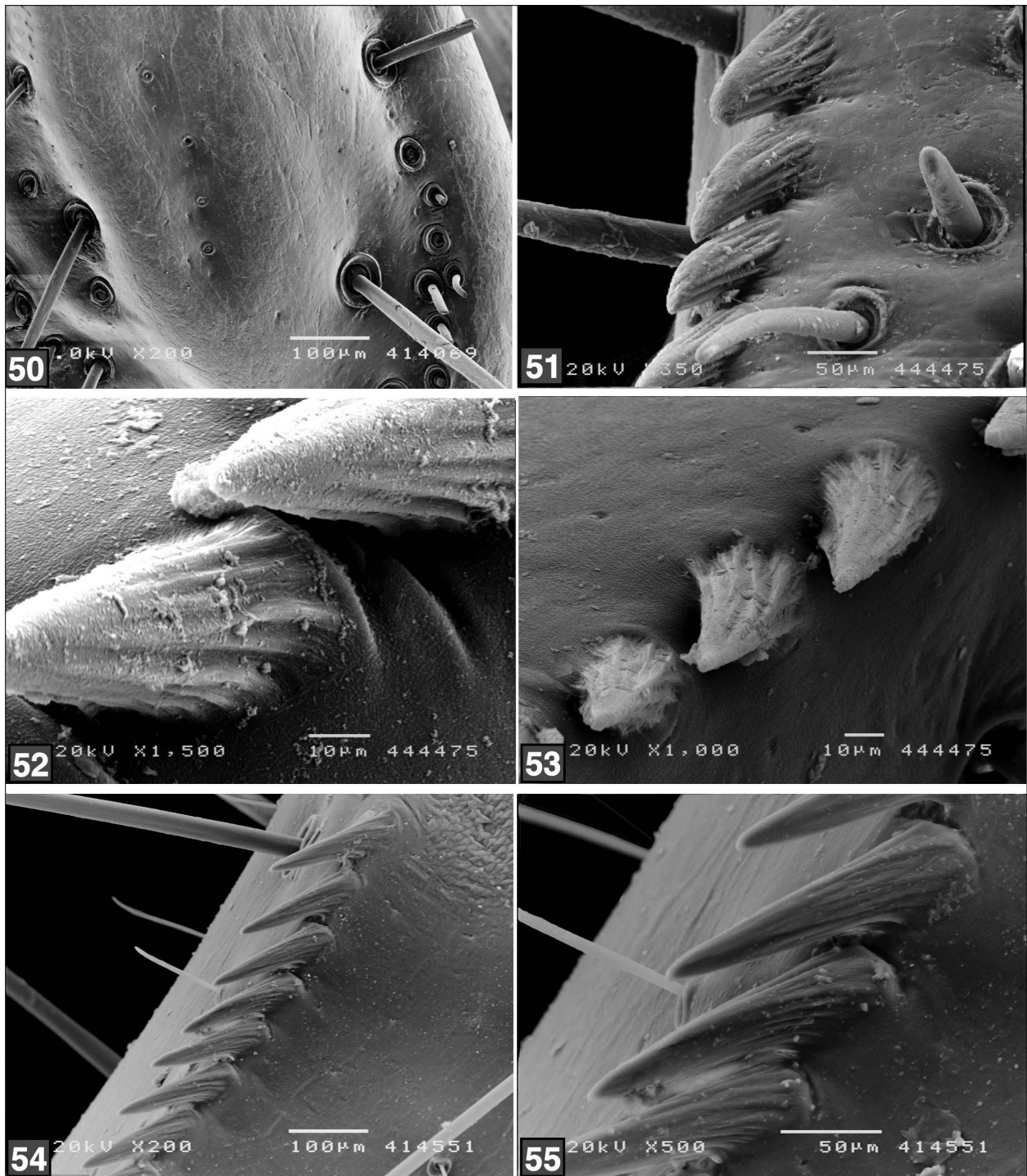
palm is deeper than wide (1.506). The sternum is wider than long (0.776). Male paratype: The carapace is shorter than the chelal movable finger (0.889), considerably shorter than metasomal segment V (0.869) and the telson (0.917). The telson is shorter than metasomal segment V (0.948). Metasomal segment 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. Soleglad) (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. Soleglad) (MES); 2 ♂, 1 ♀, Yaqui Pass Road, 3 mi. N of HWY-78, ABDSP, California, USA (33.159, -116.342; 1466'), 17 July 1996 (M. Soleglad) (MES); 1 subadult ♂, 1 adult ♀, 1 juvenile ♀, Palm Canyon Hiking Trail, primary trail (33.272, -116.425; 1036'), 16 April 1997 (M. Soleglad) (MES); 3 subadult ♂, 1 adult ♀, 2 subadult ♀, 1 juvenile ♀, Culp Valley Camp (33.224, -116.460; 3412'), 23 July 1996 (M. Soleglad) (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. Soleglad) (MES); 1 subadult ♂, 1 subadult ♀, Hellhole Hiking Trail, 1–2 mi. W of Montezuma Grade (33.241, -116.408; 1279'), 29 July 1996 (M. Soleglad) (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

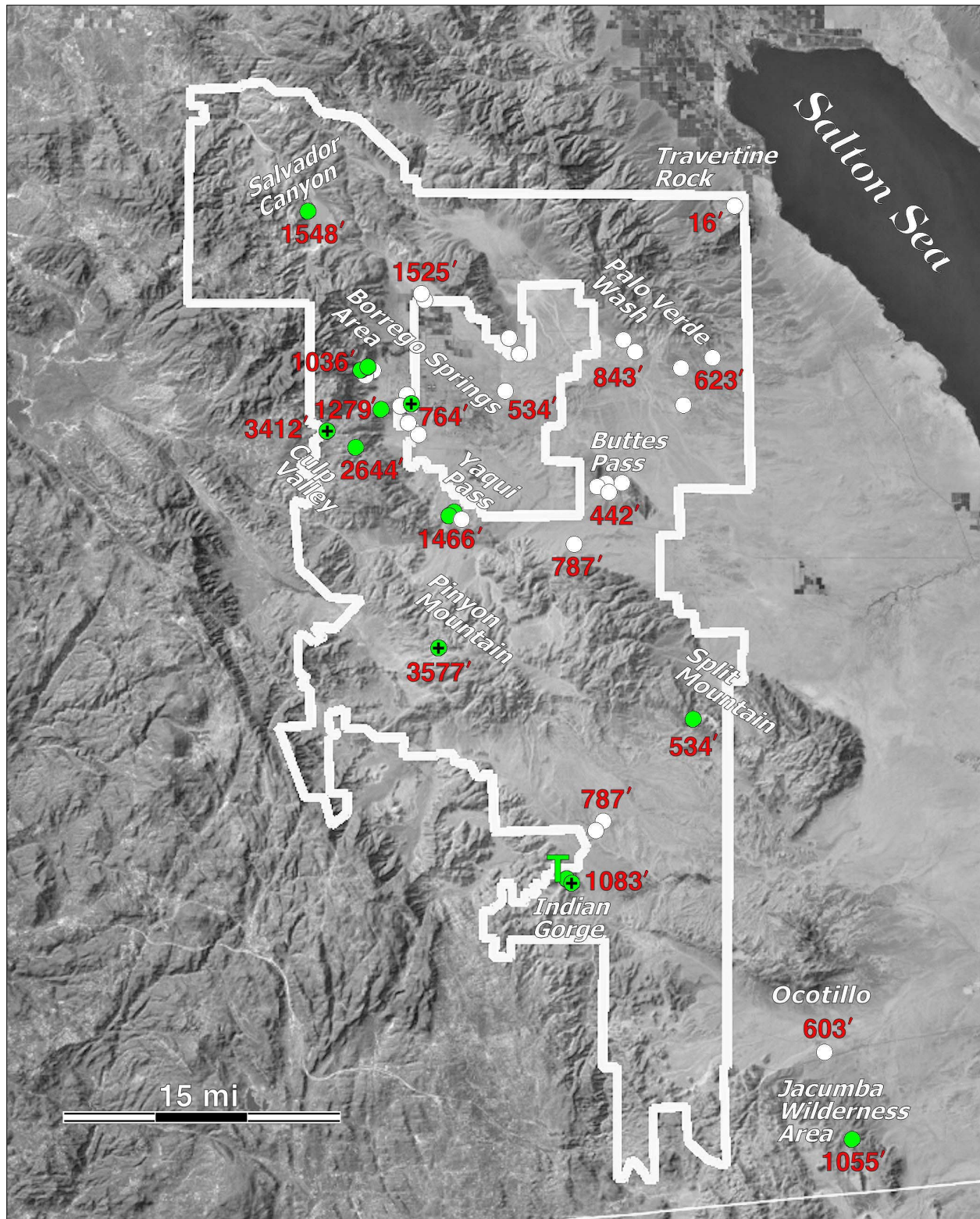


Figure 56: Distribution of *Hadrurus* species in the ABDSP vicinity as referenced in locality data. *H. anzaborrego*, **sp. nov.**, indicated with green icons (type locality marked with green T) and *H. arizonensis arizonensis* indicated with white icons. *H. anzaborrego* localities, from which DNA was analysed, are marked with an "+". 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 bajae* 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 “protohadrurine” 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 hadrurine 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 “protohadrurine” 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) *Euscorpius*, 5: 1–34.
- SOLEGLAD, M. E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.
- SOLEGLAD, M. E. & V. FET. 2008. Contributions to scorpion systematics. III. Subfamilies Smeringurinae and Syntropinae (Scorpiones: Vaejovidae). *Euscorpius*, 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 morphosculpture 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.