

USA. 7. H. arizonensis austrinus, subadult female, Oakies Landing, Baja California, Mexico. 8. H. spadix, female, Towne Pass, Purpo, Co., California, USA. 9. H. obscurus, female, Bird Spring Canyon Road, Kern Co., California, USA. 11. H. obscurus, male, Bird Spring Canyon Road, Kern Co., California, USA. 11. H. obscurus, male, Bird Spring Canyon Road, Kern Co., California, USA. 11. H. obscurus, male, Bird Spring Canyon Road, Kern Co., California, USA. 12. H. obscurus, male, Eard Spring Canyon Road, Kern Co., California, USA. 12. H. obscurus, male, Bird Spring Canyon Road, Kern Co., California, USA. 13. H. anzaborrego (dark phenotype), male, Bornego Springs, San Diego Co., California, USA. 13. H. anzaborrego (dark phenotype), male, Bornego (benetype), male, Bornego 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, Bornego Co., California, USA. 15. H. anzaborrego (dark phenotype), male, Vaqui Pass, ABDSP, San Diego Co., California, USA. 15. H. anzaborrego (dark phenotype), male, Vaqui Pass, ABDSP, San Diego Co., California, USA. 15. H. anzaborrego (pale phenotype), female, Indian Gorge Canyon, ABDSP, San Diego Co., California, USA. 15. H. anzaborrego (pale phenotype), male, Vaqui Pass, USA. 17. H. anzaborrego (pale phenotype), male, Pinyon Mountain Road, ABDSP, San Diego Co., California, USA. 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, Tecopa Hot Springs, Old Spanish Trail, Inyo Co., California, USA. 5. *H. a. arizonensis*, male, variegated phenotype, Valifornia, 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. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, pale phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*, male, phenotype, Borrego Springs, San Diego Co., California, USA. 6. *H. a. arizonensis*

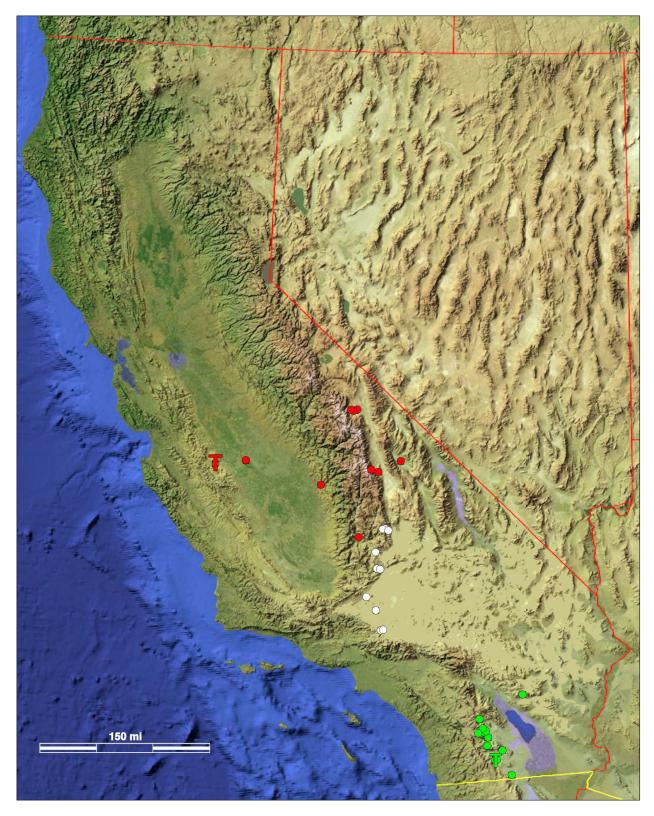


Figure 18: Distribution of three primary populations of *Hadrurus obscurus* and *H. anzaborrego*, **sp. nov.**, reported in literature and/or examined in this study. The northern population, the original Williams' (1970) records of *Hadrurus obscurus*, including type locality (red T), are indicated with 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).

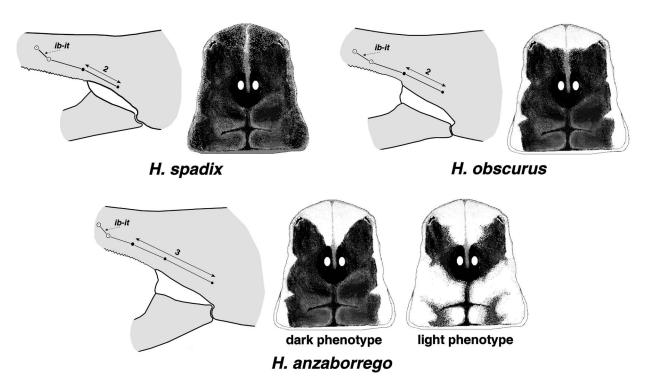


Figure 19: Diagnostic characters separating the three species of the *Hadrurus "spadix*" subgroup. Note that *H. spadix* and *H. obscurus* have two internal accessory trichobothria (dark circles) placed essentially in the same locations, whereas *H. anzaborrego* has three which are configured differently. 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-

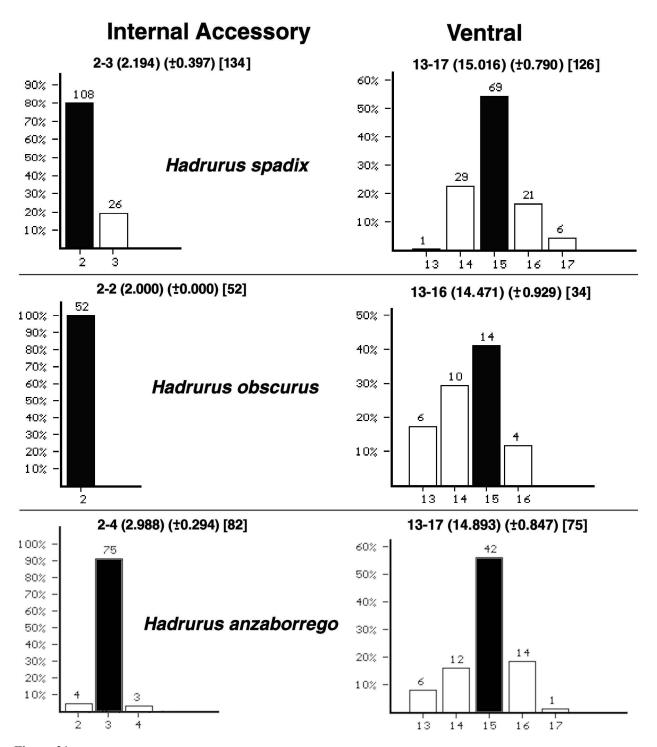
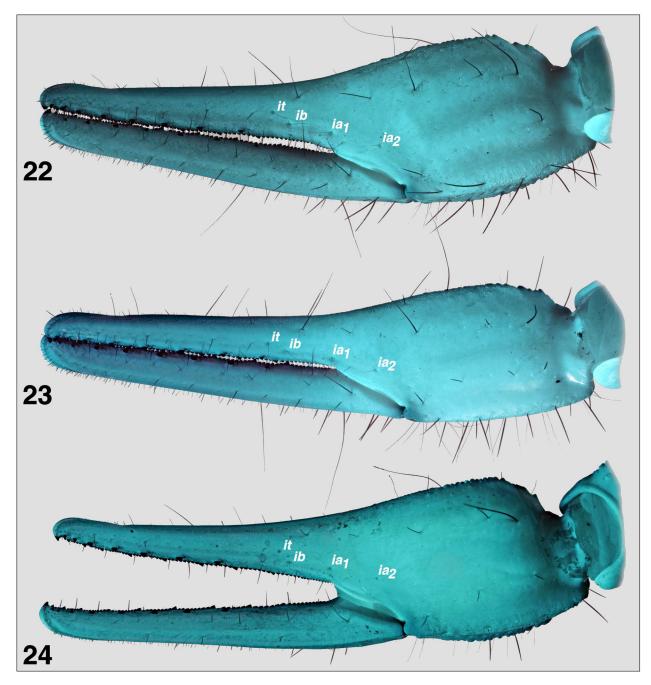


Figure 21: Chelal trichobothria statistics for the *Hadrurus "spadix*" subgroup. The data shows that *Hadrurus anzaborrego*, sp. nov., exhibits three internal accessory trichobothria, supported by over 90 % of the samples, whereas *H. obscurus* and *H. spadix* have two accessory internal trichobothria, 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 $V_I - V_4$.

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.

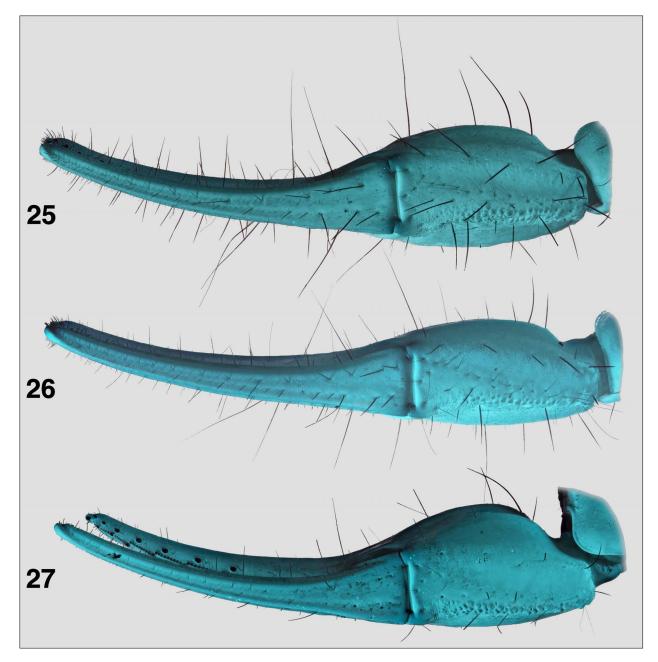
below for further information.] In *H. anzaborrego*, two color-based phenotypes are present, a dark form where the posterior half of the carapace and mesosoma is melanic, and a pale form where the wedge-shaped melanic pattern is restricted to the interocular area and mesosoma is more yellow in color.

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 "*ari-zonensis*" subgroup, the fingers are not pigmented.

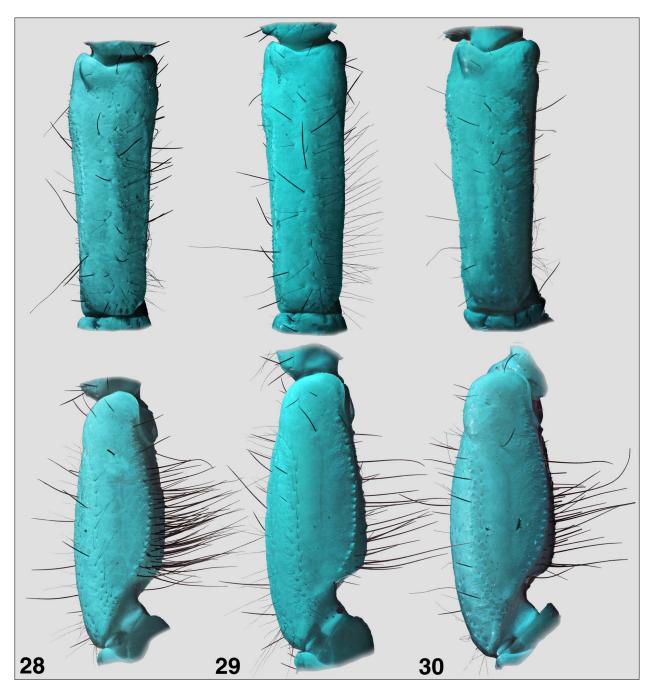
Species in Hadrurus "spadix" subgroup

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 ventromedian carinae of metasomal segments I–IV (i.e., 4-1515-6 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.