Hypsiglena chlorophaea
Desert Nightsnake

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Taxonomy. Edward D. Cope (1860b) coined the genus *Hypsiglena* for his two new species: *H. ochrorhynchus* from Cape San Lucas, Baja California, México, collected by John Xantus in 1859 (the syntypes are USNM 5283 plus eight others), and *Hypsiglena chlorophaea* from the vicinity of Fort Buchanan, AZ, by Dr. Bernard J.D. Irwin (no date; ANSP syntypes 3748–49). Cope (1887) later spelled the former as *H. ochrorhyncha* and did not recognize *H. chlorophaea*. Günther (1885–1902) referred all known species to *H. torquata*, a snake he described in 1860 originally as *Leptodeira torquata*. He noted that the holotype was collected on Isla Laguna, Lake Nicaragua, Nicaragua; however, this location is 1,850 km south of the verified southernmost location (Degenhardt *et al.* 1996). Tanner (1997) revised the type locality to near Lagunillas in Morelos, México. Boulenger (1894) included *torquata* in the genus *Hypsiglena*. Dunn (1936) placed *Hypsiglena* in synonymy with *Leptodeira*, but Taylor (1939a) revalidated *Hypsiglena* and recognized three species: *H. affinis*, *H. ochrorhyncha*, and *H. torquata*. The latter included *Liophis janii* (Dugès 1865), which Taylor (1939b) placed in synonymy with *H. t. torquata* (see *H. jani* account for details). The white and dark nuchal collar pattern of *Hypsiglena* became known as the "*torquata*-type" and the three dark blotch nuchal collar pattern as the "*ochrorhyncha*-type." Bogert and Oliver (1945) found that both nuchal patterns were sympatric in southern Sonora, México, and treated them as one species—*H. torquata*. Two species names for nightsnakes have been used in the North American reptile literature: *H. ochrorhynchus* or *H. ochrorhyncha* (*e.g.*, Cope 1892, 1900; Yarrow 1883; Stejneger and Barbour 1917 *et seq.*; Schmidt and Davis 1941; Fowlie 1965) and *H. torquata* (*e.g.*, Ditmars 1939; Schmidt 1953; Stebbins 1954, 2003; Behler and King 1979; Smith and Brodie 1982; Ernst and Ernst 2003).

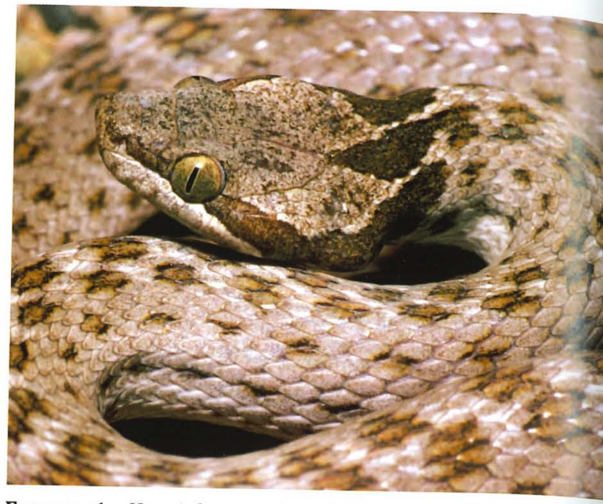

Figure 1. *Hypsiglena chlorophaea* (Desert Nightsnake) from the Maricopa Mountains, Maricopa Co. Photo by Billy Griswold.

In the first monographic treatment of the genus, Tanner (1946) recognized five species: the white-collar forms (*H. affinis*, *H. dunklei*, and *H. torquata*), the Baja California species, *H. slevini*, and the nuchal blotch pattern forms as a single species, *H. ochrorhyncha*, with multiple subspecies (*H. o. janii*, *H. o. nuchalata*, *H. o. ochrorhyncha*, *H. o. texana*, and *H. o. venusta*); *H. o. chlorophaea* was treated as synonym of *H. o. ochrorhyncha*. Tanner (1946) also described several additional subspecies, including *H. o. deserticola* and *H. o. loreala* from UT, *H. o. klauberi* from CA, and two from islands in México (*H. o. tortugaensis* and *H. o. unaocularus*). Dixon (1965) re-evaluated the *torquata*-type nuchal pattern of *Hypsiglena* and showed that some forms were sympatric with the *ochrorhyncha*-type nuchal pattern in Tamaulipas, México. He recommended recognizing two species; one for the *torquata*-type (*H. torquata*, including the subspecies *H. t. affinis*, *H. t. dunklei*, and *H. t. torquata*), and all others as *H. ochrorhyncha*, including *H. o. jani*. In a re-evaluation of the southern Sonoran contact zone, Hardy and McDiarmid (1969) returned to the recognition of only one species—*H. torquata*. Dixon and Dean (1986), in a morphological treatment of the genus (exclusive of Baja California), examined scalation and meristic characters using multivariate statistics and revealed several distinct lineages. They recommended recognizing only two species, both awaiting genetic data for clarification: the previously described *H. tanzeri* and *H. torquata* (including all other previously described subspecies). These authors recognized *H. t. ochrorhyncha* from the cape of Baja California, *H. t. jani* from central México to TX, and *H. t. chlorophaea* from Ft. Buchanan, as valid subspecies. Tanner (1985) recognized the subspecies *H. t. ochrorhyncha* and *H. t. chlorophaea* but did not consider *H. tanzeri* to represent a distinct form, thus recognizing only one species—*H. torquata*. Several researchers allied *Hypsiglena* and *Leptodeira* based on scalation and color patterns (Taylor 1938a,b; Tanner 1946; Duellman 1958a).

In a phylogeographic analysis of *Hypsiglena*, using mtDNA from ~170 individuals, Mulcahy (2008) recognized six species in what was previously considered *H. torquata*, accepted *H. tanzeri* as a full species, and found that *Eridiphas slevini* (now *H. slevini*, described by Tanner 1943) was nested within *Hypsiglena*. Five species from the *H. torquata* complex were consistent with previously described lineages (*i.e.*, subspecies), although one represented a unique, yet to be described lineage endemic to the Cochise Filter Barrier area of southeastern AZ, associated NM, and presumably northern México. Within the remaining *H. torquata* complex, *H. torquata* and *H. affinis* are restricted to México, while *H. chlorophaea*, *H. deserticola*, and *H. jani* are widespread throughout western North America, occurring in México, the United States, and southern British Columbia (Wright and Wright 1957; Mulcahy 2008). The subspecific designations for these widespread, polymorphic species were maintained because they may represent incipient species (Mulcahy 2008). Thus, three species occur in AZ: *H. chlorophaea* (including *H. c. chlorophaea* [Sonoran Nightsnake], *H. c. deserticola* [Great Basin Nightsnake], and *H. c. loreala* [Mesa Verde Nightsnake]), *H. jani texana* (Texas Nightsnake), and the Cochise clade endemic to the Cochise Filter Barrier area. Mulcahy and Macey (2009) showed that *H. chlorophaea* and the Cochise clade are closely related and were estimated to have diverged during the Pliocene Epoch, approximately 5 MYBP (see the *H. jani* account for additional information on the Cochise clade). *Hypsiglena jani* is the oldest lineage to have diverged within the *H. torquata* complex (~7.3 MYBP). A comprehensive morphological treatment of the genus, including multivariate analyses of scutellation, color patterns, and meristic data collected by W.W. Tanner, J.R. Dixon, and D.G. Mulcahy, is in progress.

Etymology. The generic name *Hypsiglena* (Gr. *hypsi*, high; Gr. *glena*, a socket, pit, or eye) is likely in reference to the prominent eyes in this snake. The specific name *chlorophaea* (Gr. *chloro*, green; Gr. *phaeo*, brown or dusky) refers to the greenish spots and brown background on the type specimen.

Description. *Hypsiglena* is a relatively small, slender-bodied snake with a distinctly narrow neck, a slightly broadened head (posteriorly) that is flat across the parietals and between the eyes, and a slightly pointed snout (Fig. 1). The pupils are elliptical and vertical. Adult *H. chlorophaea* are 240–600 mm SVL with females the larger sex (Diller and Wallace 1986; Goldberg 2001b). Record lengths include 660 mm TL (554 mm SVL) in Sonora (TCWC 47658), 605 mm TL (525 mm SVL) in British Columbia, 620 mm TL (530 mm SVL) in ID (Lacey *et al.* 1996), and 638 mm TL in WA (Weaver *et al.* 2010b). All maximum size records are for females. Mature males in ID are smaller (227–402 mm SVL, $\bar{x} = 331 \pm 5.0$, $n = 41$) than mature females (423–523 mm SVL, $\bar{x} = 494 \pm 19.0$, $n = 5$) and consequently weigh less (males 6.7–18.6 g, $\bar{x} = 12.1 \pm 0.5$, $n = 40$; females 30.7–48.7 g, $\bar{x} = 39.6 \pm 4.3$, $n = 4$; Diller and Wallace 1986). Tail length as a percentage of SVL for these samples was 15.8–23.3 ($\bar{x} = 20.5 \pm 0.2$, $n = 40$) for males and 16.3–17.6 ($\bar{x} = 17.0 \pm 0.2$, $n = 5$) for females.

There are 7–11 maxillary teeth, followed by a diastema and one or two enlarged, posterior maxillary teeth. The enlarged rear "fang" lacks a distinct groove for venom delivery (Günther

FIGURE 2. *Hypsiglena chlorophaea* (Desert Nightsnake) from the Superstition Mountains, Pinal Co. Photo by Jeffrey Martineau.

1860; Tanner 1946). However, Cowles (1941a) suggested that faint grooves, which were difficult to see, were similar to those in the close relative *Pseudoleptodeira* (Duellman 1958a; Shannon and Humphrey 1963b; Duellman 1966). Each hemipenis is single and capitate, with apical calyces and a single (non-bifurcate) *sulcus spermaticus*; the calyces and base lack spines, although there are numerous small spines distally (Duellman 1958a, 1966).

Coloration and Pattern. Hypsiglena chlorophaea is characterized by prominent, dark brown eye-jaw (postocular) stripes that may or may not connect with the dark lateral blotches on each side of the posterior portion of the head and anterior-most neck (Fig. 1). In some individuals, the stripe is prominent and continuous from the snout through the bottom half of the eye. In others, the dark pigment on the eyes and snout is much reduced. The lateral head and neck blotches are generally paired (one on each side) starting at the postocular stripe (or within 1–3 scales of it), and are 3–9 scales in length, sometimes broadening posteriorly. In some individuals, the lateral blotches connect to the middorsal blotch to form a dark collar. Lateral blotches start at scale rows 1–2 and reach scale rows 6–9. The medial blotch is usually squared posteriorly and often has a thin projection (spine) that extends anteriorly to the posterior portion of the parietals (as in most *H. c. deserticola*), but can often appear triangular as a wedge (more common in *H. c. chlorophaea*). The supralabials are generally white, sometimes with dark vertical bars that resemble teeth. The dorsal pattern is generally characterized by one or two rows of 44–78 or more dark brown, gray, or drab green spots that may or may not fuse to form a single blotch or more often are offset, forming an oblique blotch (Figs. 2–4; Tanner 1946; Hensley 1950). Dorsal body blotches are 1–3 scale rows wide and 2–7 scale rows long. Dorsal background coloration is pale gray, light brown, cinnamon-buff, cinnamon-drab, or beige. Lateral spots are usually present in two or three series of smaller spots 0.5–2 scales in width and length, alternating with the larger dorsal spots and each other. The dusky chin usually fades into a venter that is paler than the dorsal background color. Ventrals and subcaudals may or may not be flecked with small spots.

Patterns are variable among and within the three subspecies of *H. chlorophaea* that occur in AZ (Figs. 4 and 5). The typical pattern of *H. c. chlorophaea* is a three-part nuchal collar, with a median spine that is enlarged anteriorly and irregular posteriorly, forming a wedge. The eye stripe projects rearward and upward and meets, but does not connect to, the median spine. Body spots are in one or two rows. The subspecies *H. c. deserticola* typically has a median blotch that forms a rectangular box posteriorly, sometimes with a thin anterior projection and an eye-jaw stripe that projects posteriorly and slightly upward but usually does not touch the lateral blotch. There is typically one row of body spots. The subspecies *H. c. loreala* has a similar nape pattern, but with two smaller rows of dorsal spots and often lighter dorsal background coloration. Color and pattern follow Tanner (1946), Wright and Wright (1957), Ernst and Ernst (2003), and Stebbins (2003).

Scutellation. Typical head scutellation includes 2 preoculars, 2 postoculars, usually 1 loreal (sometimes 2), 2 prefrontals, usually 8 (7–9) supralabials, and usually 10 (8–12) infralabials. Temporals are larger than adjacent dorsal neck scales and typically arranged 1+2 (rarely 3). The supraoculars are narrow, and the frontal is wide. The rostral scale is pointed posteriorly and divides the prefrontals. Dorsal scales are smooth, typically in 21 rows at mid-body with some exceptions (21-19-17/15). Each dorsal scale has one apical pit, and those above the vent in males have slight keels. The cloacal scute is divided. Ventral scales numbered 164–188 ($\bar{x}$ = 178.2 ± 4.9, *n* = 136) in males and 168–195 ($\bar{x}$ = 183.2 ± 5.4, *n* = 102) in females; subcaudals were 41–62 ($\bar{x}$ = 54.7 ± 3.6, *n* = 136) in males and 24–56 ($\bar{x}$ = 47.7 ± 4.3, *n* = 102) in females (DGM, pers. obs.). In samples from AZ and northern Sonora, males had 177–194 ventrals and 49–71 subcaudals, and females had 168–191 ventrals and 42–54 subcaudals (Tanner 1946; Hensley 1950). Both ventrals and subcaudals show north-to-south clinal variation, which may reflect geographic variation in body size (Tanner 1946; Dixon and Dean 1986; Lee *et al.* 2016). There are two pairs of equal or subequal chin shields and a single mental that forms a wedge between the first pair of infralabials, completely dividing them in some individuals. Populations of *H. chlorophaea* from AZ and Sonora have higher ventral + subcaudal scale counts than those in NM, TX, and central México (Dixon and Dean 1986).

Similar Species. In AZ, *H. chlorophaea* is most easily confused with *H. jani*. However, in *H. jani* the dorsal blotches are fused more often than not to form a single middorsal row, and the elongated medial blotch on the neck is usually not connected to the lateral blotches and is narrow. Small *Arizona elegans*, *Pituophis catenifer*, or *Trimorphodon lambda* and the blotched juveniles of *Coluber constrictor* and *Senticolis triaspis* might be confused with nightsnakes where their ranges overlap. All of these snakes have round pupils except *Trimorphodon*, which has vertically elliptical pupils. *Trimorphodon lambda* also has a much larger head, more narrow neck, a lyre-shaped mark on the head, and large hexagonal dorsal blotches with a pale interior. *Arizona* and *Pituophis* have undivided cloacal scutes; the latter has four prefrontals and 27–37 keeled dorsal scales at mid-body, and the former has 25–35 smooth dorsal scales at mid-body. *Senticolis* and *Coluber* have 25 and 15–17 rows of dorsal scales at mid-body, respectively.

Distribution and Abundance. The genus *Hypsiglena* is geographically widespread, ranging from the cape of lower Baja California, the Balsas Basin and associated Pacific versant of southwestern México, and the Mexican plateau of central Hidalgo–Guanajuato to southern KS, eastern CO through the Great Basin to British Columbia, and along the West Coast to the northern reaches of the Central Valley of CA (Wright and Wright 1957; Lacey *et al.* 1996; Stebbins 2003; Matsuda *et al.* 2006; Mulcahy 2008). *Hypsiglena chlorophaea* ranges from southwestern Sonora (near Guaymas), through the Sonoran, Mojave, and Great Basin deserts bound by the eastern edges of the Peninsular Range and Sierra Nevada, north on the Columbia Plateau into British Columbia along the Okanogan River, and on the northern part of the Colorado Plateau in UT, western CO, and extreme NE AZ.

In AZ, *Hypsiglena* spp. occur virtually everywhere below 2,000 m ASL, with the fewest known locations in the northeastern and southwestern corners (Map 15), perhaps as an artifact of a general lack of collecting in these areas. *Hypsiglena c. chlorophaea* occurs from the Tucson area (as far east as the Colossal Cave area), southwest along Altar Valley, west to Yuma, and north through the Phoenix area to the northwestern part of the state south of the Mogollon Rim. Grater (1981) suggested that south of Lake Mead, *H. c. chlorophaea* (referred to as *H. t. ochrorhyncha*) occurs east of the Colorado River in AZ, whereas *H. c. deserticola* occurs west of the Colorado River in CA and NV. Further sampling and robust comparisons are needed along the Colorado River and Grand Canyon areas. There is no clear mtDNA break in this region (Mulcahy 2008). *Hypsiglena c. deserticola* also occurs northwest of Grand Canyon on the Arizona Strip. Specimens from adjacent UT suggest it also occurs in the vicinity of the Virgin River in AZ. *Hypsiglena c. loreala* occurs occurs in eastern UT and extreme southwestern CO; the morphological distinction between these two subspecies is the "usual presence" of two loreal scales in *H. c. loreala*, as opposed to one in most other *Hypsiglena*. Both *H. c. loreala* and *H. j. texana* forms have been found in extreme northeastern AZ (A.T. Holycross, pers. comm.), with *H. j. texana* occurring farther northeast than *H. c. loreala*. This suggests these two species overlap in distribution. The Cochise clade presumably contacts or overlaps *H. c. chlorophaea* north of Sonoita, Tumacacori, and Arivaca into Pima Co. and contacts or overlaps *H. jani* along the eastern border of Cochise Co. Future work in these areas is needed for a better understanding of the distributions of these species.

Questionable Localities. None.

Status and Trends. Little is known about population sizes and abundance of the genus *Hypsiglena* throughout its range. Nightsnakes are probably more common than usually thought in most areas; however, they often remain undetected because of their secretive nature (Mulcahy *et al.* 2011). Diller and Wallace (1986) found 10 *H. chlorophaea* within an intensely sampled 100 x 10 m2 area in pitfall traps in ID; *Pituophis* and *Masticophis* were more abundant. Weaver (2008) noted that *Hypsiglena* is one of the most common snakes in central WA, with as many as 5.3 snakes per 100 km of road cruising. During a long-term road-cruising survey near Phoenix, *H. chlorophaea* was almost twice as abundant on SR 238 (primarily Lower Colorado River subdivision of the Sonoran Desert) as it was on Sun Valley Parkway (primarily Arizona Upland subdivision of the Sonoran Desert; Jones *et al.* 2011b). It was six times more abundant in a relatively undisturbed area of the Sonoran Desert than in a desert/urban interface near Phoenix (Sullivan *et al.* 2017).

Habitat. *Hypsiglena chlorophaea* has been found in almost all biotic communities in AZ with the exception of Rocky Mountain Subalpine Conifer Forest, Rocky Mountain Subalpine Grassland, and Rocky Mountain Alpine Tundra, but it is found most frequently in desertscrub and grassland communities at low elevations (Lowe 1964; Hulse 1973; Jones 1981; Persons 2001; Brennan and Holycross 2006). In a study of multiple sites in a broad area of west-central AZ, Jones (1981, 1988a) documented *H. chlorophaea* in mixed broadleaf riparian, crucifixion thorn–dominated mixed shrub, juniper woodland, mesquite bosque floodplain, and Mojave Desertscrub habitats. *Hypsiglena chlorophaea* in Saguaro National Monument occurs primarily in Sonoran Desertscrub and Semidesert Grassland (Lowe and Holm 1991). It is rarely encountered in ponderosa pine forests (Weaver 2008). It typically occurs in rocky habitats, streambeds, and arroyos, often where lizards are abundant. These snakes are often associated with small rock piles, talus, and scree, decaying logs, dead Joshua tree (*Yucca brevifolia*) branches, agaves, and wood and/or trash piles. Miller and Stebbins (1964) suggested the flattened head may reflect crevice-dwelling habits. *Hypsiglena chlorophaea* occupies *Neotoma* (woodrat) middens, and *Ammospermophilus leucurus* (White-tailed Antelope Squirrel), *Dipodomys* spp. (kangaroo rats), and *Gopherus* spp. (desert tortoises) burrows (Woodbury 1948; Wright and Wright 1957; Diller and Wallace 1986). It may use aggregate dens along with multiple species of snakes (*Coluber* spp., *Crotalus viridis*, *Diadophis punctatus*, *Masticophis taeniatus*, *Pituophis catenifer*, and *Rhinocheilus lecontei*; Woodbury 1951).

In AZ, *H. chlorophaea* is typically found at about 1,000–2,000 m ASL, reaching to near 2,500 m ASL in the northern parts of the state. Some of the highest elevation records for *Hypsiglena* likely occur in AZ along the Mogollon Rim. The elevation record in Stebbins (2003), 2,650 m ASL, is likely in southern CA.

Diet and Foraging Biology. Rodríguez-Robles *et al.* (1999c) conducted a feeding ecology study of nightsnakes (*H. torquata*, *sensu lato*), examined stomach contents of nearly 400 specimens, and summarized records from field observations and the literature. The specimens examined were from throughout ranges now occupied by five different species; however, most specimens were *H. ochrorhyncha* and (secondly) *H. chlorophaea*. They found 52.2% of stomach contents were lizards, 22.8% squamate eggs, 12.0% anurans, 6.5% snakes, 3.3% insects, 1.1% *Bipes biporus* (Five-toed Worm Lizard), and 2.2 % unidentifiable items. Prey species listed in Rodríguez-Robles *et al.* (1999c) that may be encountered in AZ include juvenile *Bufo alvarius* (Sonoran Desert Toad), *Hyla arenicolor* (Canyon Treefrog), *Pseudacris* spp. (chorus frogs), *Spea multiplicata* (Mexican Spadefoot), *Aspidoscelis tigris* (Tiger Whiptail), *Coleonyx variegatus* (Western Banded Gecko), *Crotaphytus collaris* (Eastern Collared Lizard), *Gambelia wislizenii* (Long-nosed Leopard Lizard), *Holbrookia maculata* (Common Lesser Earless Lizard), *Rena dissecta*, *Rena humilis*, *Sceloporus graciosus* (Common Sagebrush Lizard), *Sonora semiannulata*, *Uta stansburiana* (Common Side-blotched Lizard), *Xantusia vigilis* (Desert Night Lizard), and squamate eggs. Of the lizards, 77.1% were diurnally active iguanian species that use cover at night but also seek shade beneath cover during the day.

Figure 3. *Hypsiglena chlorophaea* (Desert Nightsnake) from the vicinity of Tule Well, Yuma Co. Photo by Andrew T. Holycross.

Enderson (2001) observed a ~300 mm TL adult swallowing a 27 mm SUL (snout–urostyle length) juvenile *Bufo cognatus* (Great Plains Toad) at night in Maricopa Co., and found a second one of similar size in the snake after forced regurgitation. Both had been swallowed headfirst. Lance (2012) photographed an adult *H. chlorophaea* swallowing an adult *Callisaurus draconoides* (Zebra-tailed Lizard) headfirst at 0840 h in Tucson, Pima Co. Prey of *H. c. deserticola* from southwestern ID were adults and eggs of *A. tigris* and *U. stansburiana*, *Spea intermontana* (Great Basin Spadefoot), a grasshopper, and possibly a cicada (Diller and Wallace 1986). Weaver (2010b) found *Elgaria* sp. (alligator lizards), *Plestiodon skiltonianus* (Western Skink), *Sceloporus occidentalis* (Western Fence Lizard), fragments of *U. stansburiana*, *Thamnophis* sp., squamate eggs, anurans (*Pseudacris* and *Bufo*), and "clumped fur" from an unidentified small mammal among 48 identifiable prey items from 121 specimens in WA. Skinks were the most common prey. Other observations corroborate ophiophagy of *Chilomeniscus cinctus* (Brennan 2004) and *R. humilis* in AZ (Setser and Goode 2004). Kassay (1957) reported consumption of *R. humilis* and *Tantilla planiceps* (Western Black-headed Snake; reported

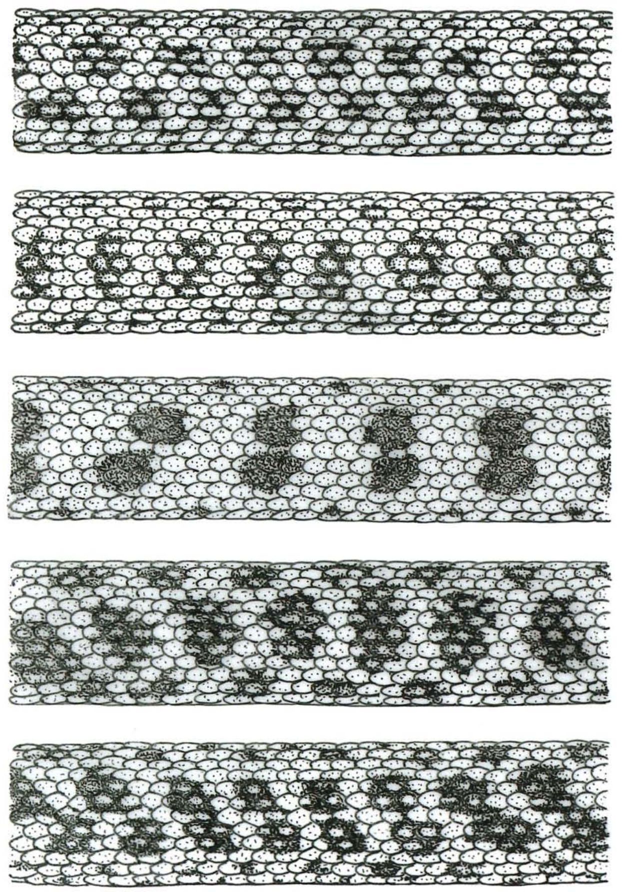

Figure 4. Dorsal patterns associated with (from top to bottom) *Hypsiglena chlorophaea chlorophaea* (Sonoran Nightsnake), *H. c. deserticola* (Great Basin Nightsnake), *H. c. loreala* (Mesa Verde Nightsnake), *H. jani texana* (Texas Nightsnake), and *H. sp.* ("Hooded Nightsnake") an undescribed species from SE AZ (Mulcahy 2008). Although the patterns illustrated above are associated with each taxon, dorsal pattern is variable and is not diagnostic. Illustration by Randall D. Babb.

as *T. eiseni*) in captivity in Riverside Co., CA. This population could represent *H. ochrorhyncha*, but it is more likely *H. chlorophaea*.

Cowles (1941a) speculated that juvenile *H. chlorophaea* take scorpions and centipedes when juvenile lizards are not available. Juvenile and adult nightsnakes preyed only on lizards in a captive study when crickets and mealworms were also offered (Dickson 1976). Adults apparently preferred lizards, whereas only juveniles ate insects (Coleoptera larva, adult Orthoptera [grasshopper], and Homoptera [cicada]; Rodríguez-Robles *et al.* 1999c). Clark (1968b) found five squamate eggs, one *U. stansburiana*, an adult weevil (Curculionidae) and one grasshopper (Orthoptera) in one individual from southern NV, but did not mention the age or size of the snake.

Based on personal field observations and reports from the literature (*e.g.*, Goodman 1953), some *Hypsiglena* actively secure prey while under cover objects during the day. Rodríguez-Robles *et al.* (1999c) suggested these snakes diurnally hunt lizards using an "ambush" strategy. Additionally, in a controlled indoor experiment, Weaver and Kardong (2009) found that *Hypsiglena* from WA showed a preference for shelter with odor of lizards or snakes versus no odor. They avoided sheltered quadrants with mouse odor. Nightsnakes lack retinal cones, visual purple, and a *fovea centralis* (Walls 1942; Underwood 1970; Stovall 1976), but instead possess three types of rods, thought to be derived from cones (Walls 1942; Stovall 1976). Additionally, the rods in *Hypsiglena* have convergent properties with the cones of *Coluber*, a diurnal snake, in low levels of light (Underwood 1970; Stovall 1976). Dickson (1976) found that nightsnakes relied more on visual cues rather than chemosensory cues, and was puzzled by the diurnal adaptations for vision in an apparently nocturnal species.

■ **Predators and Parasites.** Documented avian predators include *Buteo jamaicensis* (Red-tailed Hawk; Steenhof and Kochert 1985) and *Megascops kennicottii* (Western Screech Owl; Marshall 1957; Ross 1969). A study of *Bassariscus astutus* (Ringtail) diet on Isla San José in the Sea of Cortés recorded five instances of *Hypsiglena* consumption (Rodríguez-Estrella *et al.* 2000). Three incidences of *Hypsiglena* in the gut contents of *Lampropeltis californiae* were reported by Wiseman *et al.* (2019) and one incidence by Clark (1968b). Captive *Micruroides euryxanthus* from Maricopa Co. (Gates 1957), *L. californiae* from southern CA (Hayes 1985), and *Diadophis punctatus* from Tooele Co., UT (B. Eagar, pers. comm.), have consumed *Hypsiglena*.

In a study of endoparasites of *Hypsiglena* in AZ, Goldberg and Bursey (2001b) found that

6% of 171 specimens were infected with oligacanthorhynchid cystacanths. The infected specimens were from Maricopa and Pima counties. Additional reports of parasites in *Hypsiglena* include plerocercoids of tapeworms in the Order Proteocephalidea (Diller and Wallace 1986). As the adults require anurans or fish hosts, these authors speculated that the snakes acquired them by feeding on anurans.

■ **Behavior.** *Hypsiglena chlorophaea* is active most frequently after dark, often crossing roads during dusk. It may be active during the day beneath cover objects or hiding in rock crevices and burrows of small mammals. The activity season is April–September in ID (Diller and Wallace 1986). Over a two-year period in central WA, Weaver (2010a) found *H. c. deserticola* active April–October from 2100 to 0500 h, with males more active in May and females more active in August–September. He also found *H. c. deserticola* more active on nights with low moonlight as opposed to brighter or full moon nights. *H. chlorophaea* has been collected year-round in AZ. Wright and Wright (1957) cited the following "early appearance" and "fall disappearance" dates of activity for the subspecies: *H. c. deserticola* 20 April–28 September and *H. c. chlorophaea* 23 March–7 October. Persons (2001) found nightsnakes June–September in northern AZ; most were active on roads from 2000 h to 0400 h. Lance's (2012) observation of a nightsnake eating a lizard (see above) in Tucson was at 0840 h. Brennan's (2004) observation of predation was at 1845 h in Maricopa Co. Joseph Grinnell (*in* Van Denburgh 1922) found a *Hypsiglena* in a CA clover patch at 1600 h. Diller and Wallace (1986) reported 16 of the 21 snakes found under rocks were in pairs, with many entwined, although none were of the opposite sex. The purpose of these liaisons is unknown.

Despite the secretive nature of these snakes and lack of behavioral studies in the field, observations in captivity show a remarkable repertoire of behavioral responses to potential prey items. Dickson (1976) conducted behavioral studies

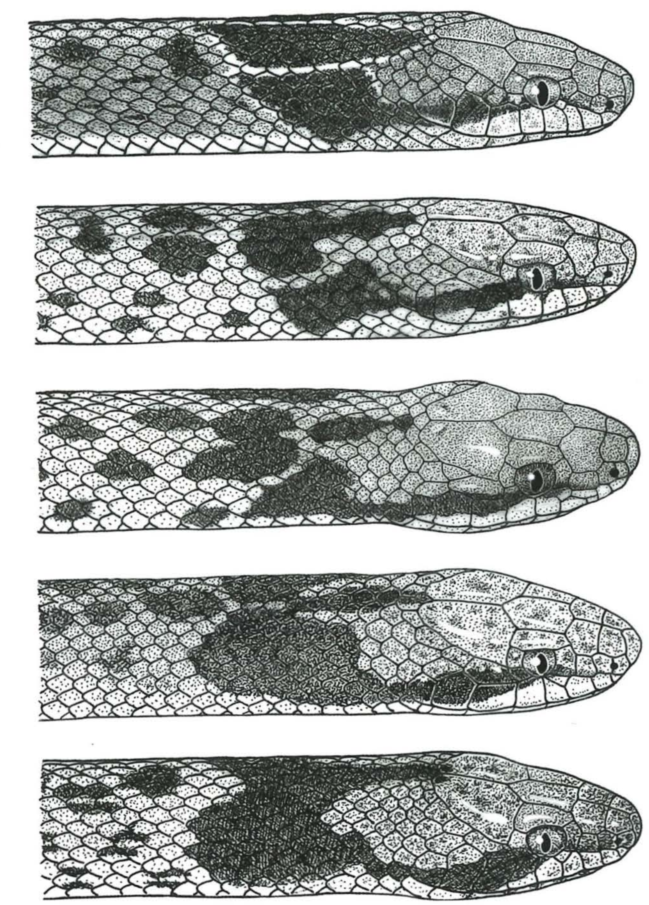

Figure 5. Facial and nuchal patterns associated with (from top to bottom) *Hypsiglena chlorophaea chlorophaea* (Sonoran Nightsnake), *H. c. deserticola* (Great Basin Nightsnake), *H. c. loreala* (Mesa Verde Nightsnake), *H. jani texana* (Texas Nightsnake), and *H. sp.* ("Hooded Nightsnake") an undescribed species from SE AZ (Mulcahy 2008). Although the patterns illustrated above are associated with each taxon, facial and nuchal pattern is highly variable and is not diagnostic. Illustration by Randall D. Babb.

of *Hypsiglena* from the Phoenix area and found responses that included: tongue flicking, neck rippling (movement of the neck in an undulatory fashion), rectilinear motion (movement in a caterpillar-like action), looping (in which coils of their body are thrown over prey to bring them closer), and striking. She also showed that a strike may occur anytime during predatory events, but there was a particular sequence containing all five behaviors that was most predominant (Fig. 6). Strikes were directed toward the head. In only 2% of trials, snakes struck without any behavior

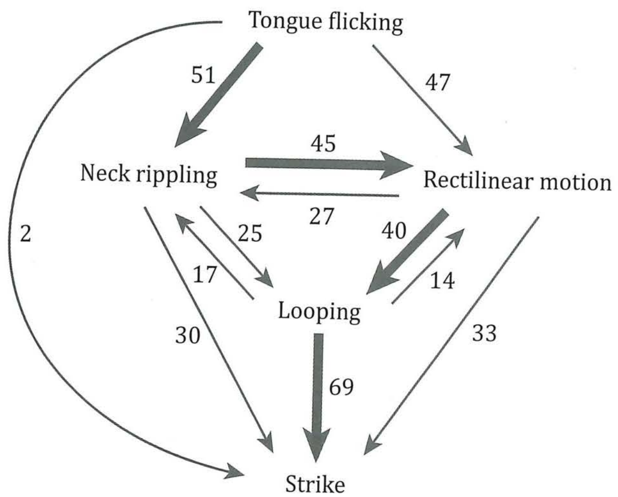

Figure 6. Behavioral responses of *Hypsiglena* (nightsnakes) to prey items (modified from Dickson 1976). Snakes showed five types of behavior with all possible sequences, but with one sequence the most common, shown by thicker lines. The frequency of going from one behavior to the next is shown beside each path.

other than tongue flicking; all attempts were unsuccessful (Dickson 1976). *Hypsiglena chlorophaea* also showed no differences in the sequence of behaviors for five different prey genera tested (*Coleonyx*, *Eumeces*, *Sceloporus*, *Urosaurus*, and *Xantusia*), but did show a preference for visual cues (*i.e.*, movement) as opposed to olfactory and auditory stimuli (Dickson 1976). She postulated that *neck rippling* and *side looping* (small loops) were attempts to mesmerize prey and that rectilinear motion enabled snakes to move closer to the prey item without attracting attention. Additionally, two adults were successful in "caudal luring," a behavior otherwise mostly confined to juveniles of several viperids (Heatwole and Davison 1976; Rabatsky 2008). *Hypsiglena* does not typically coil around prey, but Dickson (1976) found that juveniles frequently used loose coils to restrain them, a behavior that was further induced by trying to pull the lizards away.

Hypsiglena chlorophaea uses a suite of defensive behaviors in addition to simply trying to escape by rapidly crawling away or writhing when handled. Other defensive behaviors include body thrashing, forming a tight concentric coil with the head hidden in the middle, forming an S-coil, remaining inert for several minutes, waving the tail in lateral movements to attract attention away from the body, cloacal discharge, hissing, and head enlargement by flaring the maxillary and quadrate bones (Hayes 1985; Mitchell 1985; Greene 1988). These snakes rarely bite.

Reproduction. Although anecdotal reports of reproductive activities are available throughout the species' range (Hibbard 1937; Dundee 1950; Werler 1951; Gates 1957), few studies with in-depth observations have been reported in AZ (Clark and Lieb 1973; Goldberg 2001b), ID (Diller and Wallace 1986), and WA (Weaver 2010b).

Goldberg (2001b) studied reproduction in nightsnakes from AZ and included data combined from the three species that occur in AZ. Spermatogenesis occurs in males April–September (Goldberg 2001b). He pointed out that the prolonged testicular cycle fits the "B Pattern" (polyestrous with seasonal reproduction) that Saint Girons (1982) designated for tropical snakes. This was a reasonable conclusion because *Hypsiglena* is a member of a neotropical clade of snakes (Cadle 1984; see also Mulcahy 2007; Mulcahy *et al.* 2011). Natural mating dates are unknown.

Hypsiglena chlorophaea is oviparous. The shortest reproductively active male from AZ was 237 mm SVL, and the shortest female was 310 mm SVL (Goldberg 2001b). Clark and Lieb (1973) reported oviposition by a 307 mm SVL female from AZ. Size at maturity in ID was 270 mm SVL and 380 mm SVL for males and females, respectively (Diller and Wallace 1986). Females in AZ with enlarged, yolked follicles or oviductal eggs were collected April–August; known clutch size is 2–6 (Vitt 1975; Goldberg 2001b). Clutch size was 2–9 eggs in ID samples, with a positive correlation of clutch size with female body size (Diller and Wallace 1986). This was not the case for the female sample from AZ (Goldberg 2001b). Despite the fact that one female contained enlarged follicles in the fall, Goldberg (2001b) doubted that *H. chlorophaea* could produce more than one clutch per year, as speculated by Clark and Lieb (1973) and Vitt (1975). Known oviposition dates in AZ are 15 July and 1 September (Clark and Lieb 1973; Vitt 1975).

Vitt (1975) reported an average egg size of 45.3 x 12.0 mm and 4.3 g for three eggs from a female collected in Maricopa Co. Eight eggs from a female found near Ortiz, México, averaged 26.5 mm in length and 1.8 g mass (Tanner and Ottley 1981). The surface of the egg shell has not been described for *H. chlorophaea* (see *H. jani* account). Incubation time in captivity was 59 days at 20–23.9 °C for the Mexican eggs; known hatching dates were 25–26 October. Hatchling SVL were 141 mm for one male and 145 and 159 mm for two females; hatchling mass was 1.2 g and 2.0–2.1 g, respectively.

Remarks. *Hypsiglena chlorophaea* is mildly venomous (Cowles 1941a; Goodman 1953), with proteolytic venom enzymes that are most effective with lizards (Vest 1988; Hill and Mackessy 2000). Cowles (1941a) noted that lizards (*Coleonyx*, *Uta*, and *Xantusia*) bitten and chewed by *Hypsiglena* suffered from paralysis, starting at the point of injection, spreading over the entire body over 25–30 minutes; death was within ~45 minutes. Blood showed slightly reduced erythrocyte size with crenulated margins, but no sign of cell destruction; however, dissection upon death revealed a high degree of edema and loss of tonus in the skin, which appeared gelatinous in the infected area (Cowles 1941a). Other symptoms of the lizards included elevated respiration, lethargy, insensitivity to touch and pricking. Lizards were able to right themselves even though they appeared to be paralyzed (Cowles 1941a). Lewis (1946) reported similar observations for *Hypsiglena* from WA. Goodman (1953) reported an apparent diurnal ambush attack of a *Hypsiglena* (presumably *H. ochrorhyncha*) on a *Sceloporus graciosus* in the San Bernardino Mountains of southern CA. The lizard caught his attention because it was struggling in the leaf litter in the grasp of a *Hypsiglena* whose head and neck were protruding from a rock crevice. He observed the lizard's behavior for 124 minutes, but when the *Hypsiglena* attempted to drag the lizard to a hole, he picked up the snake, which then released the lizard. The lizard attempted to escape by using its forelimbs. It was easily collected. The lizard continued to occasionally wriggle the forelimbs for up to 118 minutes (after being placed in a refrigerator) and gasping for air, until it finally died approximately 120 minutes after the initial bite.

Hypsiglena rarely bites humans (Cowles 1941a; Tanner 1946); however, Russell (1980) noted a case of an *H. c. deserticola* inflicting a "painful bite" on its owner. Taub (1967) found purely serous Duvernoy's glands in this subspecies. A captive *Hypsiglena* (< 350 mm TL male) was found with the head of its apparently completely paralyzed cage mate (*Lampropeltis alterna* [Gray-banded Kingsnake], *ca.* 500 mm TL) in its mouth. Although the *L. alterna* at first appeared to have died from the interaction, it was active and healthy 20 minutes after the *Hypsiglena* was removed (D. Burkett, pers. comm. to A.T. Holycross). Gates (1951) and Hayes (1985) reported *M. euryxanthus* and *Lampropeltis getula*, respectively, feeding on *Hypsiglena* in captivity, with no apparent attempts of the *Hypsiglena* to bite its predators.

Hypsiglena is able to supercool to -5.46 °C (Lowe *et al.* 1971). A *Hypsiglena* collected in Pima Co. in August 1996 lived for 13 yr 7 mo in captivity (F.W. Eiland II, pers. comm.). Pleistocene fossils have been discovered in Mohave, Pima, Pinal, and Yuma counties, most in woodrat middens (Holman 2000).

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