

Retinal Photoreceptors and Visual Pigments in *Boa constrictor imperator*

ARNOLD J. SILLMAN,^{1*} JACQUELINE L. JOHNSON,¹ AND
ELLIS R. LOEW²

¹Section of Neurobiology, Physiology, and Behavior, Division of Biological
Sciences, University of California, Davis, California 95616

²Department of Biomedical Sciences, College of Veterinary Medicine, Cornell
University, Ithaca, New York 14853

ABSTRACT The photoreceptors of *Boa constrictor*, a boid snake of the subfamily Boinae, were examined with scanning electron microscopy and microspectrophotometry. The retina of *B. constrictor* is duplex but highly dominated by rods, cones comprising 11% of the photoreceptor population. The rather tightly packed rods have relatively long outer segments with proximal ends that are somewhat tapered. There are two morphologically distinct, single cones. The most common cone by far has a large inner segment and a relatively stout outer segment. The second cone, seen only infrequently, has a substantially smaller inner segment and a finer outer segment. The visual pigments of *B. constrictor* are virtually identical to those of the pythonine boid, *Python regius*. Three different visual pigments are present, all based on vitamin A₁. The visual pigment of the rods has a wavelength of peak absorbance (λ_{max}) at 495 ± 2 nm. The visual pigment of the more common, large cone has a λ_{max} at 549 ± 1 nm. The small, rare cone contains a visual pigment with λ_{max} at 357 ± 2 nm, providing the snake with sensitivity in the ultraviolet. We suggest that *B. constrictor* might employ UV sensitivity to locate conspecifics and/or to improve hunting efficiency. The data indicate that wavelength discrimination above 430 nm would not be possible without some input from the rods. *J. Exp. Zool.* 290:359–365, 2001. © 2001 Wiley-Liss, Inc.

A highly adaptable and very successful group of animals, the 2,300 or so living species of snakes, are very widely distributed throughout the biosphere where they fill virtually every ecological niche (Cadle, '87; Ford and Burghardt, '93; Lillywhite and Henderson, '93). Undoubtedly, their success is due to a large degree to the development of some highly sensitive sensory devices. For example, the snakes' exquisitely sensitive chemosensation is well known, and generally accepted as characteristic of all snakes. In addition, some snakes, namely the Crotalidae and the Boidae, have well-developed infrared detection systems. Their highly sensitive thermoreceptors are useful for behavioral thermoregulation, and are very important for locating and striking warm-blooded prey. This thermosense is very well integrated with yet another well-developed sensory system, that of vision. Neurons from both the heat-sensing and visual systems synapse on the same dendrites in the optic tectum of the python (Kobayashi et al., '92, '95), and there are neurons in the optic tectum of the rattlesnake that fire only when they receive signals from both thermoreceptors and photoreceptors. Indeed, a visual stimulus appears

absolutely necessary to elicit a strike by the reticulated python, whereas the strike appears to be guided by an infrared stimulus (de Cock Buning et al., '78; de Cock Buning, '83). In fact, snakes in general have relatively large and well-developed eyes and, therefore, it is not surprising that vision appears to be one of the dominant senses (Ford and Burghardt, '93). However, despite our recognition of the important role that photoreception plays in the behavior of snakes, very few studies have examined the characteristics that are basic to the function of snake photoreceptors.

In this regard, only five papers have provided data with respect to either spectral sensitivity or visual pigment absorbance in the snake retina. Using an extraction technique, Crescitelli ('56) characterized visual pigment absorbance in the rods of the viperid *Crotalus viridis helleri*. Rod

*Correspondence to: A.J. Sillman, Section of Neurobiology, Physiology and Behavior, Division of Biological Sciences, University of California, 1 Shields Avenue, Davis, CA 95616.
E-mail: ajsillman@ucdavis.edu

Received 29 January 2001; Accepted 30 April 2001

and cone absorbance was measured microspectrophotometrically in the retinas of two other viperids, *Vipera berus* and *V. lebetina*, as well as two colubrids, *Malpolon monspessulanus* and *Coronella austriaca* by Govardovskii and Chkheidze ('89). Jacobs et al. ('92) employed an electroretinographic technique to examine spectral sensitivity in the colubrid garter snakes, *Thamnophis sirtalis* and *T. marciatus*. Sillman et al. ('97) used a combination of microspectrophotometry, scanning electron microscopy and immunocytochemistry to study the visual cells of *T. sirtalis* and *T. similis*, and were able to relate specific visual pigments to morphologically distinct cones. In the most recent study, Sillman et al. ('99) used microspectrophotometry and scanning electron microscopy to characterize the photoreceptors and visual pigments of a boid, the ball python (*Python regius*). The retina of this python was found to have three different photoreceptor types, a rod containing a visual pigment with peak absorbance (λ_{\max}) at 494 nm; a relatively common, large cone containing a visual pigment with λ_{\max} at 551 nm; and a relatively rare, small cone housing an ultraviolet sensitive visual pigment with λ_{\max} at 360 nm.

The phylogenetically primitive Boidae are actually comprised of two subfamilies, the Pythoninae, or pythons, on the one hand, and the Boinae, or boas, on the other (Cogger and Zweifel, '98). The major known differences between the two groups have to do with reproduction and distribution. That is, all pythons are egg layers with most species found in the Old World, whereas all boas are viviparous with most species found in the New World (Cogger and Zweifel, '98). The 11 subspecies of *Boa constrictor*, the best-known species of boa and the subject of this study, range from central Mexico through Central America and northern South America down to Paraguay and Argentina (Cogger and Zweifel, '98; Stafford and Meyer, 2000). The intent of this study is to add to our knowledge of the functional characteristics of snake photoreceptors by extending our scanning electron microscopic and microspectrophotometric observations to the Boinae.

MATERIALS AND METHODS

For the most part, the methods employed throughout this study, along with a full description of the microspectrophotometer, have been published before (Loew and Lythgoe, '78; Loew '82; Sillman et al., '90, '91; Loew and Sillman, '93), and readers are directed to those previous studies for details; only the essentials of the methods

are given here. Colombian redtail boas (*Boa constrictor imperator*), ranging in length from 150 to 180 cm, approximately, were purchased from West Coast Reptile, Inc. (Fullerton, CA) or Glades Herp, Inc. (Fort Myers, FL), who shipped them by air to either UC Davis or Cornell. Treatment of all animals used in this study followed the guidelines for care and use of experimental animals as established by the National Institutes of Health and the American Physiological Society. The study was approved by the UC Davis Animal Care and Use Committee.

Scanning electron microscopy

Each snake was cooled with ice, stunned by a blow to the head, decapitated and the brain then pithed. Both eyes were removed, hemisected and placed in a reptilian Ringer solution, modified slightly from Secor et al. ('94) and comprised of 128 mM NaCl, 20 mM NaHCO₃, 4.7 mM KCl, 2.5 mM CaCl₂, 1.2 mM KH₂PO₄ and 1.2 mM MgCl₂. Fine forceps were then used to separate each retina from its pigmented epithelium, after which the retinas were transferred to a vial containing 3.0% glutaraldehyde (Pella, Redding, CA) in 0.1 mol/l⁻¹ phosphate buffer, pH 7.4. The retinas remained in the fixative overnight, after which they were washed with phosphate buffer, dehydrated with increasing concentrations of ethanol, and critical-point-dried. The tissue was then fragmented, mounted on a specimen stub, sputter-coated with gold, and subsequently examined with a dual-stage scanning electron microscope (ISI Model DS 130). Both positive and negative micrographs were produced using Polaroid Type 55 film. Selected micrographs were digitized with an HP Model 4C/T scanner, and the final montage created using Photoshop for Macintosh and an HP Model 4000N laser printer.

Neither dimensions nor other values obtained from the micrographs were corrected for shrinkage. We estimate shrinkage at no greater than 10%.

Microspectrophotometry

After at least 2 hr dark adaptation, snakes were killed and their retinas isolated, as described above, in a saline solution (Modified Minimum Essential Medium, Sigma, St. Louis, MO) containing either 6.0% sucrose (Sigma) or 3.0% dextran (Sigma). A small piece of retina in a drop of saline was then placed on a glass coverslip and macerated, after which a second, smaller glass coverslip was placed over the tissue and sealed to the first with silicone grease. The preparation was then positioned on

the stage of the microspectrophotometer (MSP) with the aid of very dim, deep red light. Other than this very brief (< 10 sec) exposure to visible light, all procedures were carried out using infrared illumination and image converters. Spectral absorbance data were obtained with the Cornell MSP, a computer-driven, single-beam instrument capable of accurate measurements in the near ultraviolet.

Selected absorbance curves were analyzed and wavelength of maximum absorbance (λ_{\max}) established using a programmed statistical method previously described by Loew and Sillman ('93) and Sillman et al. ('99); interested readers are directed to those papers for the details. In short, an absorbance curve was first smoothed and the smoothed data differentiated to give a preliminary estimate of λ_{\max} . The curve was then normalized to that value and converted to a normalized frequency scale (Mansfield, '85; MacNichol, '86). Linear regression was then performed on the data between 30 and 70% of λ_{\max} on the long-wavelength limb of the doubly normalized curve, and between 40 and 70% of λ_{\max} on the short-wavelength limb. The linear regression values were then compared with accepted templates for visual pigment curves derived from the rhodopsin data of Dartnall (Wysszecki and Stiles, '67) and the porphyropsin data of Bridges ('67). This procedure generated 40 estimates for λ_{\max} from the long-wavelength limb of each absorbance curve; 30 estimates from the short-wavelength limb. Mean $\lambda_{\max} \pm$ standard deviation (S.D.) was then determined using the short-wavelength limb estimates, the long-wavelength limb estimates, and the combined estimates. For each of these three λ_{\max} values, a template curve was calculated, drawn and overlaid on the original data, after which a decision as to which fitted best was made by visual examination. The template fit having the lowest S.D. usually had the best visual fit as well. After this entire procedure was carried out for each MSP curve, the λ_{\max} values for each curve of a spectral class were averaged to obtain a final estimate of mean $\lambda_{\max} \pm$ S.D. The λ_{\max} value for any one curve was included in the ultimate average for a spectral class if its calculated S.D. was less than ± 7 nm.

RESULTS

Scanning electron microscopy

The photoreceptors of *B. constrictor* are shown in Fig. 1. The retina is duplex in nature, containing both rods and cones, but greatly dominated by rods. From 12 different micrographs, we

counted 447 photoreceptors along "edges" such as those shown in Fig. 1. Of these, 50, or 11%, were cones.

The rods are typical vertebrate rods in that their inner segments are relatively narrow, and the outer segments that extend from the inner segments are long cylinders, at least over the more distal length (Fig. 1A). Also typical are the well-developed calycal processes that extend from the inner to the outer segments (small, filled arrow in Fig. 1B). The rod outer segments are rather fine, averaging only 0.94 ± 0.09 μm in diameter along the cylindrical portion (range: 0.66–1.12 μm ; $n = 50$). Because the outer segments were fragile and generally broken, we were not able to obtain reliable data with respect to outer segment length. However, judging from fragments seen in many micrographs, the rod outer segments are generally rather long. The rod outer segment denoted by the arrow in Fig. 1A appears to be intact and is about 20 μm in length. The rods are rather tightly packed. By assuming regularity, we were able to obtain an estimate of the packing density by counting rods along 'edges' in six different micrographs. Mean packing density was calculated at $280,553 \pm 84,999$ rods mm^{-2} (range: 149,454–413,873 rods mm^{-2}).

We identified two distinct types of single cone photoreceptors, both of which can be described as typical vertebrate cones. That is, both have inner segments that are globular in shape and large relative to their outer segments. The most common cone by far has a large inner segment with mean diameter, at the largest point, of 3.94 ± 0.37 μm (range: 3.05–4.45 μm ; $n = 25$), and a rather robust but relatively short outer segment (large filled arrows in Fig. 1B,C). The second type of cone (large open arrows in Fig. 1B,C) is much more rare and we saw only three. This cone has an inner segment substantially smaller in diameter than the first type; 2.89, 2.22, and 1.38 μm , respectively, in the three we observed. Its outer segment is more delicate and longer than that of the more common cone.

Microspectrophotometry

Several hundred rod and cone photoreceptors were scanned with the microspectrophotometer, revealing the presence of three different visual pigments. Analysis of the best absorbance curves recorded from rod outer segments ($n = 13$) placed the wavelength of maximum absorbance (λ_{\max}) of the rod visual pigment at 495 ± 2 nm. Fig. 2A shows a typical record taken from a rod, along with the

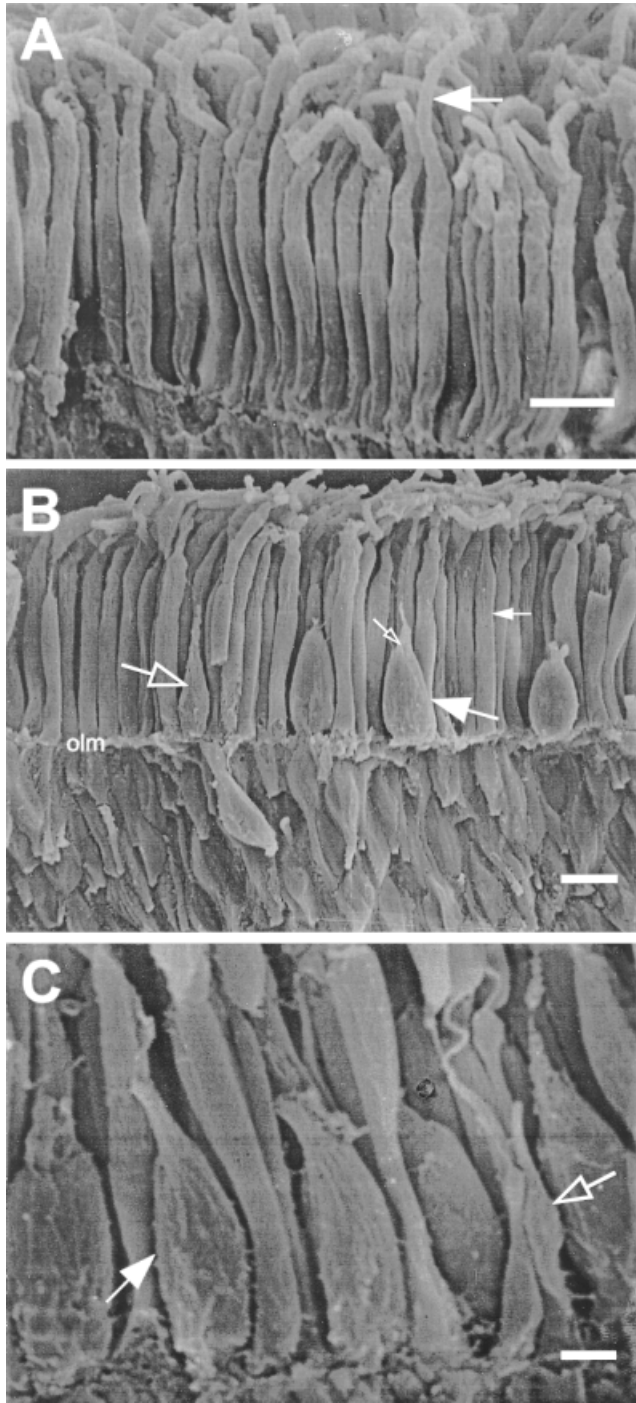


Fig. 1. Scanning electron micrographs of the photoreceptors in the retina of *Boa constrictor imperator*. (A) The arrow points to the outer segment of a rod photoreceptor. (B) OLM, outer limiting membrane. The small filled arrow points to the calycal processes of a rod; small open arrow to those of a cone. The large filled arrow points to the more common cone with large inner segment and robust outer segment; large open arrow to the more rare cone with relatively small inner segment and narrow, more delicate outer segment. (C) The filled arrow points to a large cone; open arrow to a small cone. Scale bars, 5.0 μm in A and B, 2.0 μm in C.

nomogram curve for a vitamin A₁-based visual pigment with λ_{max} at 495 nm. The most common cones, those with relatively large inner segments and rather robust outer segments, contained a vitamin A₁-based visual pigment with λ_{max} at 549 ± 1 nm ($n = 7$). The rare cones, those with a relatively small inner segment and a rather thin outer segment, contained a vitamin A₁-based visual pigment with λ_{max} at 357 ± 2 nm ($n = 3$). Typical MSP absorbance spectra for these two cone pigments, along with their nomogram curves, are shown in Fig. 2B,C, respectively. No middle-wavelength-sensitive visual pigment was ever recorded from a cone.

DISCUSSION

Photoreceptors

Our data show that the retina of *B. constrictor* is very similar to that of *P. regius*, at least with respect to the photoreceptors. Thus, the *B. constrictor* retina is duplex but highly dominated by rods, cones comprising about 11% of the photoreceptor population. This agrees very well with the 10% value for *P. regius* (Sillman et al., '99).

All the cones in the retina of *B. constrictor* are single cones, but they are of two types. By far, the majority are large cones with large inner segments and a relatively stout outer segment. Much less frequently encountered are cones with much smaller inner segments and much finer outer segments. The cone population of *B. constrictor*, then, is identical to that of *P. regius* (Sillman et al., '99). The presence of small as well as large single cones differs from the light microscopic observations of earlier investigators who reported only a single cone type in other boids (Walls, '42; Underwood, '70). This disparity could reflect species differences, but it seems more likely that the relatively rare small cone simply was missed.

B. constrictor rods, like those of *P. regius*, are long and thin and all of a single type. However, whereas in *P. regius* the cylindrical rod outer segments are similar in diameter throughout their length to the diameter of the inner segments (Sillman et al., '99), the outer segments of *B. constrictor* rods taper to a thinner cylinder. Since the relatively thick inner segment of the *B. constrictor* rods limits the packing density, the thinner tips cannot reduce the grain of the image and, therefore, do not confer any advantage in terms of increased visual acuity. In fact, the mean packing density of *B. constrictor* rods at $280,553 \pm 84,999$ cells mm^{-2} is substantially less than that of *P. regius* rods at $457,740$ cells mm^{-2} (Sillman et al., '99). *B. constrictor*'s rod packing density is a

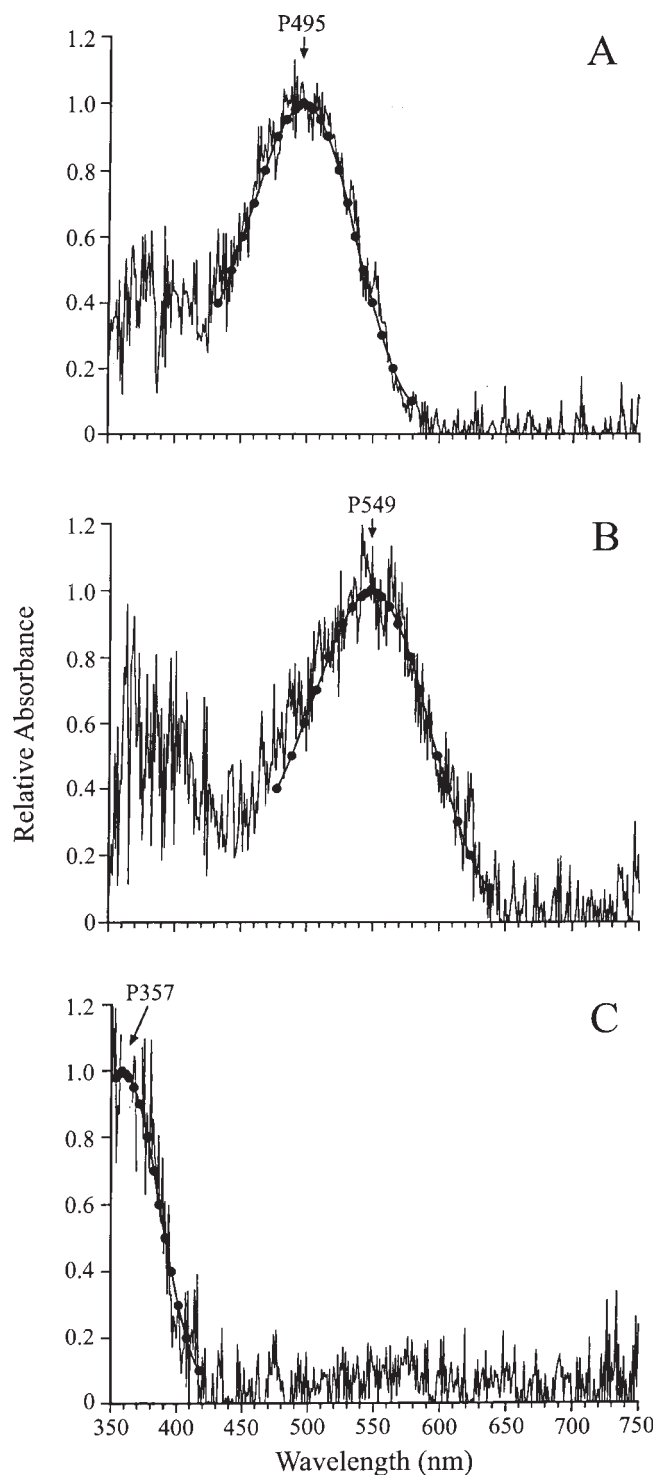


Fig. 2. Typical normalized absorbance curves, obtained with the microspectrophotometer, from the photoreceptors of *Boa constrictor imperator*. (A) Absorbance curve from a rod shown with the nomogram curve for a vitamin A₁-based visual pigment with peak absorbance (λ_{\max}) at 495 nm (circles and smooth line). (B) Absorbance curve from a long-wavelength-sensitive cone shown with the nomogram curve for a vitamin A₁-based visual pigment with λ_{\max} at 549 nm (circles

and smooth line). (C) Absorbance curve from an ultraviolet-sensitive cone shown with the nomogram curve for a vitamin A₁-based visual pigment with λ_{\max} at 357 nm (circles and smooth line). Actual peak absorbance values are 0.034, 0.025, and 0.023 optical density units for A, B and C, respectively.

bit on the low side when compared to other nocturnal creatures as well. For example, rod packing density has been measured at 275,000–460,000 rods mm^{-2} in the cat *Felis domesticus*, depending on the region measured (Steinberg et al., '73); 310,000–485,000 rods mm^{-2} in the North American opossum *Didelphis virginiana* (Kolb and Wang, '85); 216,000–478,000 rods mm^{-2} in the owl monkey *Aotes trivirgatus* (Ogden, '75); 374,000–400,000 rods mm^{-2} in the albino laboratory rat (Cone, '63; Mayhew and Astle, '97). These data suggest that *B. constrictor*'s nocturnal visual sensitivity and acuity might be somewhat less than that of *P. regius* and other nocturnal animals, but certainly good enough for orientation towards forms and, especially, moving objects. Moreover, the upper value for *B. constrictor* rod packing density (413,873 rods mm^{-2}) compares very well with the values for the nocturnal animals noted above.

Acute vision under bright light conditions should also be of importance to *B. constrictor*, since the snake is described as diurnal as well as nocturnal. It is an ambush predator whose prey includes diurnal lizards and birds (Stafford and Meyer, 2000). In this regard, it is significant that the 8:1 rod:cone ratio we found in *B. constrictor* reflects a cone packing density of about 35,000 cones mm^{-2} . Although less than that found in either *P. regius* (50,000 cones mm^{-2} ; Sillman et al., '99) or the owl monkey (78,000 cones mm^{-2} ; Ogden, '75), it is far greater than cone packing density in the area centralis of the North American opossum (8000 cones mm^{-2} ; Kolb and Wang, '85) and, given the variability in our measurements, at least as great as cone packing density in the area centralis of the cat (27,000 cones mm^{-2} ; Steinberg et al., '73). Visual resolution, of course, is not dependent solely on cone packing density; factors such as optics, retinal magnification, cone-to-ganglion cell convergence, and cone sampling, are also important (e.g., Pettigrew et al., '88). However, strictly on the basis of cone packing density, it is reasonable to conclude that the photopic visual resolution of *B. constrictor* is similar to that of the cat. The cat's photopic visual acuity is about nine cycles degree⁻¹ (Jacobson et al., '76). Although far less than that of the human (60 cycles degree⁻¹; Pettigrew et al., '88), such resolution would undoubtedly allow formation of a highly useful image.

and smooth line). (C) Absorbance curve from an ultraviolet-sensitive cone shown with the nomogram curve for a vitamin A₁-based visual pigment with λ_{\max} at 357 nm (circles and smooth line). Actual peak absorbance values are 0.034, 0.025, and 0.023 optical density units for A, B and C, respectively.

Visual pigments

The visual pigments of *B. constrictor* are virtually identical to those of *P. regius* (Sillman et al., '99). Thus, the visual pigment in *B. constrictor* rods absorbs maximally at 495 ± 2 nm; *P. regius* 494 ± 2 nm. The long wavelength-sensitive visual pigment in *B. constrictor*'s common, large cone has a λ_{max} at 549 ± 1 nm; *P. regius* 551 ± 3 nm. The ultraviolet-sensitive visual pigment in *B. constrictor*'s rare, small cone has λ_{max} at 357 ± 2 nm; *P. regius* 360 ± 3 nm. All visual pigments, in both species, are based on vitamin A₁. Both boid snakes studied thus far, then, lack the middle wavelength-sensitive cone pigment (λ_{max} 482 nm) found in the phylogenetically more advanced colubrid snake, *T. sirtalis* (Sillman et al., '97).

The absence of a middle wavelength-sensitive cone pigment might severely limit the ability of *B. constrictor* (and *P. regius* as well) to discriminate wavelengths. Although the main and *cis* absorbance bands of the 549 nm and 357 nm pigments allow a fairly broad spectral sensitivity, the fact that the 357 nm pigment does not overlap the 549 nm pigment beyond 430 nm, and does not contribute to visual sensitivity beyond 430 nm (Jacobs, '92), points to the absence of wavelength discrimination beyond 430 nm. However, as Sillman et al. ('99) suggested for *P. regius*, it is possible that the rods of *B. constrictor*, with maximum sensitivity at 495 nm, interact with the cones to substantially extend the spectral range over which the snake might see color. Both rods and cones are active under the mesopic light levels characteristic of dawn and dusk, and rods are known to contribute to color vision under those conditions (Reitner et al., '91; Stabell and Stabell, '94; Buck, '97). Sillman et al. ('99) speculated that the partially transmuted nature of *P. regius* rods, if true, might allow those cells to function both as highly sensitive rods and as middle wavelength-sensitive cones. This conjecture is applicable to *B. constrictor* as well.

Ultraviolet sensitivity

B. constrictor becomes the third snake, along with *T. sirtalis* and *P. regius*, in which an ultraviolet-sensitive cone has been identified (Sillman et al., '97, '99). Ultraviolet sensitivity is now known to be rather widespread in the animal kingdom (Jacobs, '92) and, therefore, one must assume that the capability has important adaptive value, especially considering that ultraviolet light can damage retinal tissues (Jacobs, '92; Bennett and Cuthill, '94).

Of course, in the simplest sense, ultraviolet-sensitive cones would have value merely by extending the range of spectral sensitivity. It is, however, the possibility that ultraviolet sensitivity might play an important role beyond broadening the spectral sensitivity curve that has aroused the most interest. With respect to such a role in snakes, Sillman et al. ('97) suggested that *T. sirtalis* might use its ultraviolet sensitivity to locate scent trails deposited by conspecifics. Since pythons are also known to leave scent trails (Slip and Shine, '88), Sillman et al. ('99) extended the idea to *P. regius*, and further speculated that *P. regius* might improve its hunting efficiency by locating paths preferred by its small mammalian prey—paths marked by increased contrast due to either the reflection or absorption of ultraviolet light. Some rodents do indeed excrete urine and feces that reflect ultraviolet light and, in fact, the Eurasian kestrel *Falco tinnunculus* uses that ultraviolet light to locate voles (Desjardins et al., '73; Viitala et al., '95).

B. constrictor could utilize its ultraviolet sensitivity to similar advantage. A trail left by a conspecific could be located visually, again because of the contrast due to either reflection or absorption of ultraviolet light. The snake would then identify and follow the source with the use of its highly sensitive chemosensitive system. In like manner, *B. constrictor* would be able to detect ultraviolet active components, either reflective or absorptive, in excretions of the lizards and small mammals which comprise much of its diet. The snake could then establish its ambush position at a spot frequented by its prey. This would certainly improve hunting efficiency, especially in a snake that is described as sluggish (Stafford and Meyer, 2000). Moreover, some lizards are known to reflect substantial ultraviolet light from portions of the skin surface (Fleishman et al., '93), and many birds, also a prey item for *B. constrictor* (Stafford and Meyer, 2000), have plumage with significant ultraviolet reflectance (Bennett and Cuthill, '94). In both cases, contrast between the prey animal and the surround would be increased, making the potential target more obvious to the snake and thereby improving hunting efficiency. This is especially important when one considers that the most important single stimulus for arousing *B. constrictor* and initiating hunting activity is a visual stimulus (de Cock Buning, '83).

ACKNOWLEDGMENTS

The authors wish to thank Mr. Steven Asercion for his assistance in producing the figures, and

Mr. Michael Dunlap of the UC Davis Facility for Advanced Instrumentation for his technical assistance with the scanning electron microscope.

LITERATURE CITED

- Bennett AT, Cuthill IC. 1994. Ultraviolet vision in birds: what is its function? *Vision Res* 34:1471–1478.
- Bridges CDB. 1967. Spectroscopic properties of porphyropsins. *Vision Res* 7:349–369.
- Buck SL. 1997. Influence of rod signals on hue perception: Evidence from successive scotopic contrast. *Vision Res* 37:1295–1301.
- Cadle JE. 1987. Geographic distribution: problems in phylogeny and zoogeography. In: Seigel RA, Collins JT, Novak SS, editors. *Snakes: Ecology and Evolutionary Biology*. New York: Macmillan. p 77–105.
- Cogger HG, Zweifel RG. 1998. *Encyclopedia of Reptiles and Amphibians*, 2nd edition. San Diego: Academic Press. 240 p.
- Cone RA. 1963. Quantum relations of the rat electroretinogram. *J Gen Physiol* 46:1267–1286.
- Crescitelli F. 1956. The nature of the gecko visual pigment. *J Gen Physiol* 40:217–231.
- de Cock Buning T. 1983. Thermal sensitivity as a specialization for prey capture and feeding in snakes. *Am Zool* 23:363–375.
- de Cock Buning T, Poelmann RE, Dullemeijer P. 1978. Feeding behaviour and the morphology of the thermoreceptors in *Python reticulatus*. *Neth J Zool* 28:62–93.
- Desjardins C, Maruniak JA, Bronson FH. 1973. Social rank in house mice: differentiation revealed by ultraviolet visualization of urinary marking patterns. *Science* 182:939–941.
- Fleishman LJ, Loew ER, Leal M. 1993. Ultraviolet vision in lizards. *Nature* 365:397.
- Ford NB, Burghardt GM. 1993. Perceptual mechanisms and the behavioral ecology of snakes. In: Seigel RA, Collins JT, editors. *Snakes: Ecology and Behavior*. San Francisco: McGraw-Hill. p 117–164.
- Govardovskii VI and Chkheidze NI. 1989. Retinal photoreceptors and visual pigments in certain snakes. *Biol Abstr* 90:1036.
- Jacobs GH. 1992. Ultraviolet vision in vertebrates. *Am Zool* 32:544–554.
- Jacobs GH, Fenwick JA, Crognale MA, Deegan II JF. 1992. The all-cone retina of the garter snake: spectral mechanisms and photopigment. *J Comp Physiol A* 170:701–707.
- Jacobson SG, Franklin KBJ, McDonald WI. 1976. Visual acuity of the cat. *Vision Res* 16:1141–1143.
- Kobayashi S, Kishida R, Goris RC, Yoshimoto M, Ito H. 1992. Visual and infrared input to the same dendrite in the tectum opticum of the python, *Python regius*: electron-microscope evidence. *Brain Res* 597:350–352.
- Kobayashi S, Amemiya F, Kishida R, Goris RC, Kusunoki T, Ito H. 1995. Somatosensory and visual correlation in the optic tectum of a python, *Python regius*: a horseradish peroxidase and Golgi study. *Neurosci Res* 22:315–323.
- Kolb H, Wang HH. 1985. The distribution of photoreceptor, dopaminergic amacrine cells and ganglion cells in the retina of the North American opossum (*Didelphis virginiana*). *Vision Res* 25:1207–1221.
- Lillywhite HB, Henderson RW. 1993. Behavioral and functional ecology of arboreal snakes. In: Seigel RA, Collins JT, editors. *Snakes: Ecology and Behavior*. San Francisco: McGraw-Hill. p 1–48.
- Loew ER. 1982. A field-portable microspectrophotometer. In: Packer L, editor. *Methods in Enzymology*, Vol. 81H. New York: Academic Press. p 647–654.
- Loew ER, Lythgoe JN. 1978. The ecology of cone pigments in teleost fishes. *Vision Res* 18:715–722.
- Loew ER, Sillman AJ. 1993. Age-related changes in the visual pigments of the white sturgeon (*Acipenser transmontanus*). *Can J Zool* 71:1552–1557.
- MacNichol EF Jr. 1986. A unifying presentation of photopigment spectra. *Vision Res* 26:1543–1556.
- Mansfield, RJW. 1985. Primate photopigments and cone mechanisms. In: Fein A, Levine JS, editors. *The Visual System*. New York: Liss. p 89–106.
- Mayhew TM and Astle D. 1997. Photoreceptor number and outer segment disk membrane surface area in the retina of the rat: stereological data for whole organ and average photoreceptor cell. *J Neurocytol* 26:53–61.
- Ogden TE. 1975. The receptor mosaic of the *Aotes trivirgatus*: distribution of rods and cones. *J Comp Neurol* 163:193–202.
- Pettigrew JD, Dreher B, Hopkins CS, McCall MJ, Brown M. 1988. Peak density and distribution of ganglion cells in the retina of microchiropteran bats: implications for visual acuity. *Brain Behav Evol* 32:39–56.
- Reitner A, Sharpe LT, Zrenner E. 1991. Is colour vision possible with only rods and blue-sensitive cones? *Nature* 352:798–800.
- Secor SM, Stein ED, Diamond J. 1994. Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation. *Am J Physiol* 266:G695–G705.
- Sillman AJ, Spanfeller MD, Loew ER. 1990. The photoreceptors and visual pigments in the retina of the white sturgeon, *Acipenser transmontanus*. *Can J Zool* 68:1544–1551.
- Sillman AJ, Ronan SJ, Loew ER. 1991. Histology and microspectrophotometry of the photoreceptors of a crocodilian. *Alligator mississippiensis*. *Proc R Soc Lond Ser B* 243:93–98.
- Sillman AJ, Govardovskii VI, Röhlich P, Southard JA, Loew ER. 1997. The photoreceptors and visual pigments of the garter snake (*Thamnophis sirtalis*): a microspectrophotometric, scanning electron microscopic and immunocytochemical study. *J Comp Physiol A* 181:89–101.
- Sillman AJ, Carver JK, Loew ER. 1999. The photoreceptors and visual pigments in the retina of a boid snake, the ball python (*Python regius*). *J Exp Biol* 202:1931–1938.
- Slip DJ, Shine R. 1988. The reproductive biology and mating system of diamond pythons, *Morelia spilota* (Serpentes: Boidae). *Herpetologica* 44:396–404.
- Stabell U, Stabell B. 1994. Mechanisms of chromatic rod vision in scotopic illumination. *Vision Res* 34:1019–1027.
- Stafford PJ, Meyer JR. 2000. *A Guide to the Reptiles of Belize*. San Francisco: Academic Press. 356 p.
- Steinberg RH, Reid M, Lacy PL. 1973. The distribution of rods and cones in the retina of the cat (*Felis domesticus*). *J Comp Neurol* 148:229–248.
- Underwood, G. 1970. The eye. In: Gans C, editor. *Biology of the Reptilia, Morphology B*, Vol. 2. New York: Academic Press. p 1–97.
- Viitala J, Korpimäki E, Palokangas P, Kolvula M. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* 373:425–427.
- Walls GL. 1942. *The Vertebrate Eye and Its Adaptive Radiation*. Bloomfield Hills, MN: Cranbrook Press. 785 p.
- Wyszecki G, Stiles WS. 1967. *Color Science*. New York: Wiley. 628 p.