

Spectral transmittance of the spectacle scale of snakes and geckos

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Abstract

The spectral transmittance of the optical media of the eye plays a substantial role in tuning the spectrum of light available for capture by the retina. Certain squamate reptiles, including snakes and most geckos, shield their eyes beneath a layer of transparent, cornified skin called the 'spectacle'. This spectacle offers an added opportunity compared with eyelidded animals for tailoring the spectrum. In particular, the hard scale that covers the surface of the spectacle provides a unique material, keratin, rarely found in vertebrate eyes, a material which may have unique spectral properties. To verify this, shed snake and gecko skins were collected and the spectral transmittance of spectacle scales was spectrophotometrically analyzed. The spectacle scale was found generally to behave as a highpass filter with a cut-off in the ultraviolet spectrum where taxonomic variation is mostly observed. The spectacle scales of colubrid and elapid snakes were found to exhibit higher cut-off wavelengths than those of pythonids, vipers, and most boids. Gecko spectacle scales in turn exhibited exceptional spectral transmittance through the visual spectrum down into the UV-B. It is suggested that this is due to the absence of beta-keratins in their spectacle scale.

Contents

Introduction	1
Material and methods	2
<i>Sample collection</i>	2
<i>Spectrophotometry</i>	0
<i>Thickness measurements</i>	3
<i>Analytical methods</i>	3
Results	3
<i>Snake spectacle scale transmittance</i>	3
<i>Gecko spectacle scale transmittance</i>	3
<i>Spectacle scale thickness</i>	5
<i>Relationship between spectacle scale thickness and $\lambda_{50\%}$</i> ..	5
Discussion	5
<i>Spectacle scale transmittance: taxonomic variation</i>	5
<i>Considering the spectacle scale's role as an optical filter</i> ..	7
<i>Considering the spectacle scale's role as mechanical barrier</i>	8
<i>Gecko versus snake spectacle scales and a discussion of keratin composition</i>	8

Conclusion	9
Acknowledgements	9
References	9

Introduction

The optical media of the eye play a crucial role in tuning the spectrum of light incident upon the retina. For example, tissues may filter out short wavelengths of the blue and ultraviolet (UV) ranges to increase image contrast or block harmful radiation, such as occurs with the yellow crystalline lenses of some squirrels (Walls, 1931; Chou and Cullen, 1984), squamate reptiles (Walls, 1942; Röhl *et al.*, 1996; Röhl, 2000) and fishes (Walls and Judd, 1933; Kennedy and Milkman, 1956; Muntz, 1973).

The spectral transmittance and absorption of various ocular media (*i.e.* the cornea, lens, neural retina, and aqueous and vitreous humours) have been studied in all vertebrate taxa (reviewed in Douglas and Marshall, 1999), although data on reptiles remains somewhat limited (Ellingson *et al.*, 1995; Bowmaker *et al.*, 2005), and the reptilian spectacle, despite its unique position in the optics of squamate eyes, has received surprisingly little attention (Safer *et al.*, 2007; Hart *et al.*, 2012).

The spectacle is a layer of transparent skin that covers the eyes of many squamates, including all snakes and most geckos (Fig. 1; Walls, 1942). Despite being the primary window through which these animals see, very few studies have investigated the spectral properties of the spectacle. Hart *et al.* (2012) and Safer *et al.* (2007) respectively reported on the transmittance of hydrophid sea snake spectacles and rattlesnake spectacle scales, the former measuring in the visible and UV range while the latter focused on the infrared spectrum, which is not of visual relevance. Given the unusual nature of the reptilian spectacle as an extra layer in the

has a higher $\lambda_{50\%}$ than all crotaline vipers (331 nm versus a mean of 317 nm). These findings warrant further investigation to determine if they are representative of their respective subfamilies.

Spectacle scales' $\lambda_{50\%}$ correlates with their thickness although it's unclear if thickness is the cause and $\lambda_{50\%}$ the effect. The association may be indirect by virtue of both being characteristic of certain families, begging the question of why colubrid spectacle scales generally are thicker and have higher $\lambda_{50\%}$ than other families, elapids and specific boids excluded. Also, according to the Spearman's Rho of 0.784, $\lambda_{50\%}$ and thickness are not perfectly related, so other factors may be at play here. To speculate on this, a consideration of the functional adaption of spectacle scale $\lambda_{50\%}$ and thickness is called for.

Considering the spectacle scale's role as an optical filter

Coloured 'filters' are present in the eyes of many species: the pigmented or iridescent corneas of numerous reef fish, the yellow lenses of some fish, squirrels and diurnal reptiles, the macula lutea of primates, and the photoreceptor oil droplets of birds and reptiles (Walls, 1942; Lythgoe, 1979; Douglas and Marshall, 1999; Hart, 2001). These are often associated with diurnal activity and are suggested to block harmful short wavelength radiation, to improve image contrast by removing shorter wavelengths that are more likely to scatter, or in the case of oil droplets to fine tune photoreceptor absorbance spectra to improve colour discrimination (reviewed in Douglas and Marshall, 1999). The spectacle scale's contribution to overall transmittance of the eye is limited in most species to blocking the mid to far UV-A and UV-B, excepting the Snouted Cobra, Hognose Snake, and adult Spine-Bellied Sea Snake (*Lapemis curtus* (Shaw, 1802), Hart *et al.*, 2012), all of which block much UV-A and some of the blue region of the spectrum.

While the UV-A region spans a broad range from 315-400 nm, vision in this region will be restricted to the specific spectral absorbances of an animal's retinal opsins. Several species of snake and gecko are known to possess UV-A sensitive cones (Loew, 1994; Ellingson *et al.*, 1995; Loew *et al.*, 1996; Sillman *et al.*, 1997, 1999, 2001; Davies *et al.*, 2009; Macedonia *et al.*, 2009; Yang, 2010; Hart *et al.*, 2012), suggesting that the visual perception of UV-A wavelengths is a common trait throughout these taxa. The retinal absorbance spectra of four snakes included in this study have

been previously characterized (*Thamnophis sirtalis* (Sillman *et al.*, 1997), *Python regius* (Sillman *et al.*, 1999), *Boa constrictor* (Sillman *et al.*, 2001), and *Masticophis flagellum* (Macedonia *et al.*, 2009)) with each found to possess a UV-sensitive opsin with a peak absorbance near 360 nm, which is above the $\lambda_{50\%}$ of all their spectacle scales but is remarkably close to it in the case of the Coachwhip Snake (max $\lambda_{50\%}$ = 355 nm). *T. sirtalis* and the Coachwhip Snake are also known to possess yellow lenses (Walls, 1931) which likely provide further UV blockage.

The spectacle scale's position as the initial optical filter may be advantageous in that it obviates the need for soft tissues vulnerable to intense radiation to perform this function. However, only in colubrids, elapids, and the odd boid does the spectacle scale attenuate short wavelength UV, indicating that any ocular filtration that might occur in the other boids and in vipers and pythons will nevertheless be accomplished by cellular tissues or the humours. While UV is implicated in cataract development and retinal damage (Sloney, 1986; Taylor, 1989; Gelatt *et al.*, 2013), it has also been implicated in damage of the ocular surface itself, as in certain cases of conjunctival neoplasms and keratitis (Wu *et al.*, 2006; Gelatt *et al.*, 2013). In humans, UV may also influence the development of pterygium which is characterized by anomalous growth of conjunctival tissue from the sclera or limbus over and into the corneal surface (Moran and Hollows, 1984). Mechanisms to minimize radiation-induced damage to the ocular surface should therefore be present in most species exposed to some amount of UV. For the species that bear it, the spectacle may be one such protective structure. One may hypothesize that the coachwhip snake's sharp $\lambda_{50\%}$ at ~350 nm may have been an adaptation to its diurnal activities in arid habitats, but the evidence is circumstantial as most colubrids in this study, diurnal or not, and regardless of habitat, have high cut-offs (genus *Lampropeltis* being the curious exception). Given that several of the vipers in this study (North and Central American rattlesnakes) are deserticolous and active diurnally during some seasons (Landreth, 1973; Golan *et al.*, 1982), it would have been compelling were their spectacle scales to exhibit high $\lambda_{50\%}$ as a protective barrier to UV, but this is clearly not the case. A tangential, but interesting correlation in this regard is the presence of slit or near-slit pupils among the vipers, boas and pythons compared with the rounded pupils of all the sampled colubrids and elapids. Because the crystalline lenses of many colubrids (*e.g.* genera *Masticophis*, *Coluber*, *Elaphe*) protrude through the pupil, a lower limit

is set upon the constricted pupil diameter (*Lampropeltis* can constrict its pupil to rather small dimensions [see photo in Coborn, 1991: 251]). Vipers, boas and pythons are not limited in this regard and can constrict their pupils to smaller areas. While the pupil obviously plays no role in tuning the spectrum, it nevertheless regulates the absolute luminous flux within the eye, which may be protective in itself. An investigation of diurnally-active slit-pupilled colubrids (e.g. some members of subfamily Lycodontinae such as *Oligodon ornatus* Van Denburgh, 1909) may shed light on whether such a correlation exists between pupil shape and spectacle transmittance.

The conspicuous coloration of the snouted cobra's yellow spectacle stands out in recalling the yellow lenses and corneas of some diurnal terrestrial vertebrates, including the lenses of some snakes and geckos (Walls, 1931; Walls and Judd, 1933; Walls, 1942) and the lenses and corneas of certain fishes (Walls and Judd, 1933; Walls, 1942; Kennedy and Milkman, 1956; Muntz, 1973), which are suggested to function as barriers to UV and/or to increase retinal image contrast. The snouted cobra is not unique among snakes in possessing a yellow spectacle however as the adult Spine-Bellied Sea Snake's spectacle blocks short wavelengths to a similar degree as the snouted cobra and, remarkably, to a much greater degree than the juvenile form of the species as reported by Hart *et al.* (2012). Because Hart *et al.* (2012) reported on the whole spectacle, dermis and scale together, it is unknown which layer accounts for the attenuation. The somewhat brown colouration of the hognose snake spectacle scale as observed in this study may also function as a modest filter. The chemical nature of spectacle scale colouration is not known, but may conceivably be related to its specific keratin isoforms or fiber arrangement or it may be contributed by pigments deposited in the scale during keratogenesis or alternatively, it may result from staining by the animals' substrate, such as by tannins or quinone pigments. Spectrophotometric measures and biochemical analyses on shed skins collected in the field or from captive animals kept on specific substrates would be valuable in determining the influence of environmental stains on spectacle scale pigmentation.

Considering the spectacle scale's role as mechanical barrier

In addition to blocking more deep UV-A, a thicker spectacle scale will offer greater protection against physical injury during locomotion. Walls' (1942) anecdote about observing '... the sadly scratched and dull appearance

of the spectacle of a garter snake inhabiting such an abrasive place as a stone wall' is particularly relevant here; habitat and exposure of the eyes/spectacles due to morphology or method of locomotion may influence evolution of spectacle scale thickness and/or mechanical resistance. Another risk to eyes comes from prey or prey conspecifics disagreeing with the snakes' intentions. This is well illustrated by Bonnet *et al.*'s (1999) account of a population of Island Tiger Snake (*Notechis scutatus* (Peters, 1861)) with a disproportionately high incidence of blindness caused by adult gulls protecting their nests. In this light, it is perhaps notable that colubrids generally have thicker spectacle scales than vipers, boas and pythons. The colubrid species investigated in this study lack the vipers' envenomation mechanisms to subdue prey or deter predation, and they similarly lack the boas and pythons overall large size (though there is some overlap in body size, e.g. bull/pine snakes and Puerto Rican Boas).

In regard to the gecko spectacle scale, it is perhaps not surprising that it is so thin since the two species investigated in this study are arboreal insectivores. Unlike snakes who force their heads through abrasive substrate, geckos' eyes rarely encounter anything more harmful than a small shoot or a leaf.

Gecko versus snake spectacle scales and a discussion of keratin composition

Compared with those of snakes, gecko spectacle scales exhibit extraordinarily high transmittance. Though thinner than snakes' at 3-4 μm , they are not much thinner than a Mojave rattlesnake's (5 μm), yet the latter's transmittance profile parallels those of other vipers, including the strong attenuation of UV-B and the much smaller peak at 254 nm. The Marbled Gecko (*Gekko grossmanni*) is largely nocturnal, requiring little need for protection from UV radiation. Indeed if UV is visually relevant to this species, the absence of UV filtration may be advantageous to maximize photon capture. The diurnal Giant Day Gecko (*Phelsuma madagascariensis grandis*) in contrast will be exposed to as much UV as many diurnal snakes, yet its spectacle scale lets pass a tremendous dose of UV. The gecko spectacle scale appears quite simply to have evolved for maximal transmittance. To reiterate the notion that one must consider the whole eye's spectral transmittance in evaluating an animal's visual capabilities, it should be noted that despite this admission of UV through the gecko spectacle scale, the Giant Day Gecko's retina is nevertheless well shielded (or benefitted by a contrast filter) by virtue of a yellow

lens (Tansley, 1961). It is not unique in this regard as many diurnal geckos possess yellow lenses (Röll *et al.*, 1996; Röll and Schwemer, 1999; Röll, 2000, 2001).

The spectral properties of a material are related to the chemical composition of that material, and spectacle scales are known to vary in their keratin composition according to family, subfamily, and even between conspecifics and between hatchlings and juveniles (van Doorn *et al.*, 2014). The absence of beta-keratin in gecko spectacle scales (van Doorn *et al.*, 2014) is perhaps most accountable for the observed differences between snake and gecko spectacle transmittance. With their exceptionally high transmittance profiles that parallel published alpha-keratin spectra (horse hair: Bendit and Ross, 1961; human stratum corneum: Bruls *et al.*, 1984), gecko spectacle scales appear to exist at the highest limit of what keratins can transmit. The spectacle scales of snakes, in contrast, attenuate shorter wavelengths in the UV-A and particularly in the UV-B, and will even block or scatter longer wavelengths as evidenced by their gradually tapering transmittance curves. Beta-keratin, for all its beneficial contributions to mechanical protection, does appear to limit spectral transmittance somewhat. It should be borne in mind that the measures reported here were on shed scales which will have been scratched and pitted during the routine activities of the animals (attesting to their protective role!). This may account for some of the spectral attenuation with decreasing wavelength as optical scatter is inversely related to wavelength, but it is unlikely to account for the complete blockage of short wavelength UV-A, UV-B and the reduction or obliteration of the 254 nm peak in the UV-C (which though not biologically relevant to earthbound animals nevertheless reflects differences in the material).

Another example of keratin's influence on spectral transmittance may be seen in the reticulated python hatchling, whose first shed post-hatch, corresponding with the embryonic integument, exhibits a slightly different transmittance profile, particular around 320 nm where the trace shows a 'hump' not otherwise seen in the juvenile or adult sheds. Though it wouldn't be visually relevant, it may reflect the different beta-keratin complement of the embryonic integument compared with more mature animals (van Doorn *et al.*, 2014).

Conclusion

The contribution of the spectacle scale to the spectral properties of the eye varies significantly between taxa,

even down to the species-level in some cases. While its effect on the whole eye transmittance of some species may be insignificant (*e.g.* geckos, vipers, pythons, most boas), in others it may play a substantial role in tuning the visual spectrum (*e.g.* Snouted Cobra, Hognose Snake) or blocking harmful short wavelengths (*e.g.* colubrids with sharp cut-offs such as the Coachwhip Snake). Further research is warranted on other families and subfamilies of both snake and gecko of different ecologies. Biochemical analyses may be valuable in determining how keratin isoforms affect transmittance and to determine the nature of the colouration in some spectacle scales.

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Table 1. Sampled species from which shed spectacle scales were collected and measured, including their 50% cut-off wavelengths ($\lambda_{50\%}$) and thicknesses. Thickness measurements are not available for some samples for reasons explained in the text.

Family	Subfamily	Species	Common name	$\lambda_{50\%}$ (nm)	Thickness (μm)
Gekkonidae	Gekkoninae	<i>Gekko grossmanni</i> Günther, 1994	Marbled gecko	243	4
Gekkonidae	Gekkoninae	<i>Phelsuma madagascariensis</i> (Gray, 1831)	Giant day gecko	246/266	3
Boidae	Boinae	<i>Boa constrictor</i> Linnaeus, 1758	Boa Constrictor	317	20
Boidae	Boinae	<i>Boa constrictor</i>	Boa Constrictor	314	16
Boidae	Boinae	<i>Boa dumerili</i> (Jan in Jan and Sordelli, 1860)	Dumeril's Boa	308	15
Boidae	Boinae	<i>Boa dumerili</i>	Dumeril's Boa (juvenile)	308	14
Boidae	Boinae	<i>Corallus hortulanus</i> (Linnaeus, 1758)	Garden Tree Boa	305	
Boidae	Boinae	<i>Epicrates inornatus</i> (Reinhardt, 1843)	Puerto Rican Boa	318	12
Boidae	Boinae	<i>Eunectes murinus</i> (Linnaeus, 1758)	Green Anaconda	361	
Boidae	Erycinae	<i>Charina bottae</i> (Blainville, 1835)	Rubber Boa	351	18
Colubridae	Colubrinae	<i>Bogertophis subocularis</i> (Brown, 1901)	Transpecos Ratsnake	336	20
Colubridae	Colubrinae	<i>Drymarchon couperi</i> (Holbrook, 1842)	Indigo Snake	350	50
Colubridae	Colubrinae	<i>Elaphe guttata</i> (Linnaeus, 1766)	Corn snake	339	25
Colubridae	Colubrinae	<i>Elaphe guttata</i>	Corn snake (juvenile)	339	18
Colubridae	Colubrinae	<i>Elaphe obsoleta</i> (Say in James, 1823)	Black Ratsnake	347	19
Colubridae	Colubrinae	<i>Elaphe obsoleta</i>	Black Ratsnake	354	
Colubridae	Colubrinae	<i>Elaphe obsoleta</i>	Black Ratsnake	334	
Colubridae	Colubrinae	<i>Elaphe obsoleta</i>	Black Ratsnake	344	
Colubridae	Colubrinae	<i>Elaphe obsoleta lindheimeri</i> (Baird and Girard, 1853)	Texas rat snake (leucistic)	355	38
Colubridae	Colubrinae	<i>Elaphe obsoleta lindheimeri</i>	Texas Rat snake (leucistic)	358	
Colubridae	Colubrinae	<i>Elaphe taeniurus</i> Cope, 1861	Beauty snake	343	33
Colubridae	Colubrinae	<i>Elaphe taeniurus</i>	Beauty snake	347	30
Colubridae	Colubrinae	<i>Elaphe taeniurus</i>	Beauty Snake	347	31
Colubridae	Colubrinae	<i>Lampropeltis alterna</i> (Brown, 1901)	Grey-banded Kingsnake	313	19
Colubridae	Colubrinae	<i>Lampropeltis alterna</i>	Grey-banded Kingsnake	333	20
Colubridae	Colubrinae	<i>Lampropeltis alterna</i>	Grey-banded Kingsnake	312	14
Colubridae	Colubrinae	<i>Lampropeltis mexicana thayeri</i> Loveridge, 1924	Thayer's Kingsnake	326	20
Colubridae	Colubrinae	<i>Lampropeltis triangulum hondurensis</i> K.L. Williams, 1978	Honduran Milksnake	342	
Colubridae	Colubrinae	<i>Masticophis flagellum flagellum</i> (Shaw, 1802)	Eastern Coachwhip	355	40
Colubridae	Colubrinae	<i>Masticophis flagellum flagellum</i>	Eastern Coachwhip	340	
Colubridae	Colubrinae	<i>Masticophis flagellum flagellum</i>	Eastern Coachwhip	350	50
Colubridae	Colubrinae	<i>Masticophis flagellum testaceus</i> (Say in James, 1823)	Western Coachwhip	354	
Colubridae	Colubrinae	<i>Pituophis catenifer</i> (Blainville, 1835)	Gopher Snake	348	46
Colubridae	Colubrinae	<i>Pituophis catenifer</i>	Gopher Snake	344	30
Colubridae	Colubrinae	<i>Pituophis melanoleucus</i>	Bullsnake	349	38
Colubridae	Colubrinae	<i>Pituophis melanoleucus</i> (Daudin, 1803)	Bullsnake	344	35
Colubridae	Colubrinae	<i>Pituophis melanoleucus</i>	Bullsnake	350	30
Colubridae	Colubrinae	<i>Pituophis melanoleucus</i>	Northern Pine Snake	350	
Colubridae	Colubrinae	<i>Pituophis melanoleucus</i>	Northern Pine Snake	351	50
Colubridae	Colubrinae	<i>Pituophis melanoleucus</i>	Southern Pine Snake	349	35
Colubridae	Colubrinae	<i>Pituophis melanoleucus lodingi</i> Blanchard, 1924	Black Pine Snake	357	
Colubridae	Colubrinae	<i>Pituophis ruthveni</i> Stull, 1929	Louisiana Pine Snake	348	
Colubridae	Colubrinae	<i>Spilotes pullatus</i> (Linnaeus, 1758)	Tiger Rat Snake	356	
Colubridae	Colubrinae	<i>Thamnophis sirtalis parietalis</i> (Say in James, 1823)	Red-sided garter snake	338	21
Colubridae	Xenodontidae	<i>Heterodon platirhinos</i> Latreille in Sonnini and Latreille, 1801	Hognose Snake	381	
Colubridae	Xenodontidae	<i>Heterodon platirhinos</i>	Hognose Snake (juvenile)	406	31
Colubridae	Xenodontidae	<i>Heterodon platirhinos</i>	Hognose Snake (juvenile)	360	25
Elapidae		<i>Dendroaspis polylepis</i> (Günther, 1864)	Black Mamba	342	

cont. Table 1.

Family	Subfamily	Species	Common name	$\lambda_{50\%}$ (nm)	Thickness (μm)
Elapidae		<i>Naja annulifera</i> Peters, 1854	Snouted Cobra	415	
Elapidae		<i>Naja pallida</i> Boulenger, 1896	Red Spitting Cobra	343	
Pythonidae		<i>Morelia amethystina</i> (Schneider, 1801)	Amethystine Python	310	16
Pythonidae		<i>Morelia spilota</i> (Lacépède, 1804)	Carpet Python	313	
Pythonidae		<i>Morelia spilota</i>	Carpet Python	312	19
Pythonidae		<i>Morelia spilota</i>	Carpet Python	320	18
Pythonidae		<i>Morelia viridis</i> (Schlegel, 1872)	Green Tree Python	305	13
Pythonidae		<i>Python molurus bivittatus</i> Kuhl, 1820	Burmese Python	308	20
Pythonidae		<i>Python molurus bivittatus</i>	Burmese Python	329	10
Pythonidae		<i>Python molurus bivittatus</i>	Burmese Python (juvenile)	319	15
Pythonidae		<i>Python regius</i> (Shaw, 1802)	Ball Python	309	15
Pythonidae		<i>Python reticulatus</i> (Schneider, 1801)	Reticulated Python (first shed)	312	15
Pythonidae		<i>Python reticulatus</i>	Reticulated Python (juvenile)	326	14
Pythonidae		<i>Python reticulatus</i>	Reticulated Python (juvenile)	318	13
Pythonidae		<i>Python reticulatus</i>	Reticulated Python (juvenile)	334	
Pythonidae		<i>Python sebae</i> (Gmelin, 1788)	Rock Python	322	
Pythonidae		<i>Python sebae</i>	Rock Python	327	21
Viperidae	Crotalinae	<i>Agkistrodon bilineatus</i> Günther, 1863	Mexican Mocassin	310	15
Viperidae	Crotalinae	<i>Agkistrodon bilineatus</i>	Mexican Mocassin	325	15
Viperidae	Crotalinae	<i>Bothrops neuwiedi</i> Wagler, 1824	Jararaca Pintada	324	14
Viperidae	Crotalinae	<i>Crotalus basiliscus</i> (Cope, 1864)	Mexican West Coast Rattlesnake	317	
Viperidae	Crotalinae	<i>Crotalus durissus vegrandis</i> Klauber, 1941	Uracoan Rattlesnake	310	15
Viperidae	Crotalinae	<i>Crotalus mitchellii pyrrhus</i> (Cope, 1867)	Southwestern Speckled Rattlesnake	320	
Viperidae	Crotalinae	<i>Crotalus oreganus helleri</i> Meek, 1905	Southern Pacific Rattlesnake	319	
Viperidae	Crotalinae	<i>Crotalus scutulatus</i> (Kennicott, 1861)	Mojave Rattlesnake	307	5
Viperidae	Crotalinae	<i>Crotalus atrox</i> Baird and Girard, 1853	Western Diamondback	320	
Viperidae	Crotalinae	<i>Trimeresurus erythrurus</i> (Cantor, 1839)	Redtail Viper	303	
Viperidae	Viperinae	<i>Bitis gabonica</i> (Duméril, Bibron and Duméril, 1854)	Gaboon Viper	331	22