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ROM TWO TO 10 EYELASH VIPERS! WHAT IS GOING ON IN THE TAXONOMIC WORLD?

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*Photos by the author, unless otherwise stated.

The eyelash viper *Bothriechis schlegelii* (Berthold, 1846) is one of the most famous snakes in the world. It is known from southern Mexico throughout Meso and Central America and into South America.

west of the Andes to the northwestern tip of Peru. One of the most notable characteristics of the species is its high chromatic variability. It is probably the most variable species on the planet.

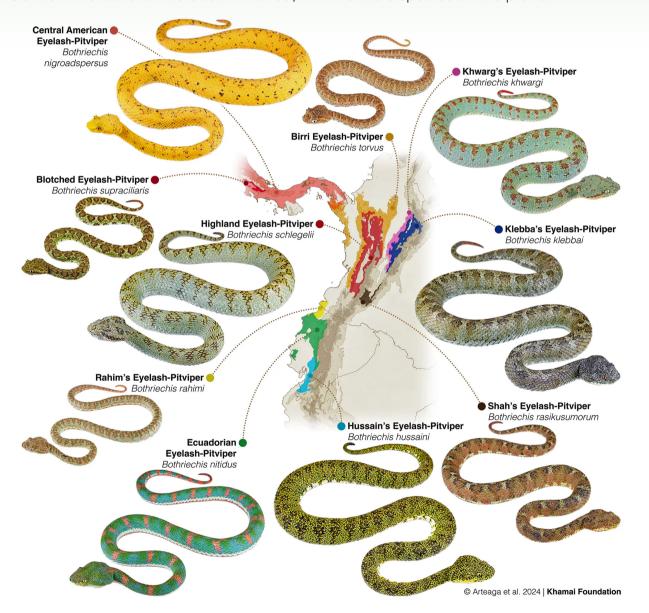


Figure 1. Distribution Map of the Bothriechis schlegelii complex with representatives of each species. Image from Arteaga et al. (2024), with permit.

When I lived in Venezuela (from 1995 to 2011) I was trying to solve the mystery of whether the species was present in the country. Curiously, to date, no one has been able to do it. The report comes from two or three totally vaque records. Pifano et al. (1950) based their observation on a gravish specimen with a white anterior ventral part, apparently from Ureña, an enclave of dry vegetation in the state of Táchira. The coloration is really unusual for the species (gray without any type of marking) even with our knowledge of the enormous polychromatic variation of which it is capable. Very curious is that the specimen (certainly extraordinary) was never deposited in any official collection. Also strange is the habitat, as the species never has been reported from a xeric region. Later, in 1965, Sandner-Montilla (1965) reported it again from the state of Amazonas without any type of explanation! Obviously, biogeographically it is totally impossible to believe that such species could be in the middle of the Venezuelan Amazon. Well, Sandner-Montilla was known as a funny (and problematic) guy, and Campbell & Lamar (2004) acknowledged him for many years of laughs!

However, the reports remained floating in the air, carried over and perpetuated

by subsequent authors (Hoge & Lancini, 1962; Lancinii, 1979; Roze, 1966). Even after having discussed it with my colleagues and co-authors of the latest list of reptiles of Venezuela (Rivas et al., 2012) and despite my personal contrary decision, the species was kept on the list. Only Natera et al. (2015) shows the lack of data to maintain that the species occurs in Venezuela. Finally, Arteaga et al. (2024), after discussing this matter extensively with me, completely ruled out its presence from that country.

In 2010 I moved to Costa Rica, one of the herpetological paradises in the world, and without a doubt, one of the goals I had when I arrived was to observe an "oropel" (yellow phase eyelash viper, which means in Spanish: piel de oro= golden skin) in its habitat. I managed to do this quickly. On my first day walking in a forest in the southern Caribbean, there it was, spectacular, radiant, clearly visible, as if it was telling me "come and photograph me!"

Soon, I began to find different morphs; the white one, the pink one, all sorts of greens and all in the southern Caribbean. Then I moved to the Pacific, where there is also a great variety of chromotypes. One of the most colorful and



Figure 2. B. supraciliaris from San Vito, Puntarenas, Costa Rica.

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Figure 3. B. nigroadspersus pink, Caribbean Costa Rica, courtesy of Quetzal Dwyer.

common is known as the "Christmas tree" which is dark green with red, orange and white spots, but there are also many grayish and cryptic varieties in the Pacific as well (aside from "oropels"). The variety is so wide that it never gets boring.

I was also interested in finding the highaltitude "bocaracá" *Bothriechis supraciliaris* (Taylor, 1954) that occurs on the Pacific slope of the Talamanca Mountain Range. This species also has a great variety of morphs, although not as many as the lowland species. I knew that a few "oropels" had been reported in this species and I managed to see them. Since then, living in Costa Rica, I have been able to observe an impressive array of colorations of both species.

On my travels through Central and South America I was able to learn about other varieties of the eyelash viper in Guatemala, Panama, Colombia and Ecuador... and the conclusion was always the same; they didn't look like the ones in Costa Rica! Either they were more robust, or had less developed supraciliary scales, or even with completely differentiable shapes.

In Ecuador, together with Alejandro Arteaga, Lucas Bustamante and other colleagues, in a border area with Colombia in the Chocoan rainforest, we saw 2 "oropels" (vellow phase evelashes) that for me were not a big surprise, since in Costa Rica they are everywhere, but for them it was the first time ever reported of such yellow eyelash vipers in the country! Also with them, in another Chocoan locality, I was able to discover the green morph so typical of western Ecuador. In Colombia, I had the opportunity to learn about several varieties as well, both in Popayan, Quindío and Santander, addina to the notion that all these varieties were not only simple variants, but rather they should be different species and that a comprehensive morphological and molecular work should be completed. So, 10 years ago, together with Alejandro Arteaga, who would masterfully lead the work with colleagues and friends, the collection of data began. I will present these results later.

At the Alexander Koening
Museum in Bonn, Germany, together
with Claudia Koch, we reviewed the
holotype, believed to have been lost since
World War II, of *Trigonocephalus schlegelii*Berthold, 1846. Verifying that it was a juvenile,
and using ancient DNA extraction methods,
it could be sequenced molecularly. The same
happened with another important holotype,
that of *Bothrops* (*Teleuraspis*) nigroadspersus
Steindachner, 1870, which is in the Natural
History Museum of Vienna.

In the end, together with all these colleagues and other great herpetologists, Alejandro was conducting this symphony of new knowledge, until finally, in 2024, the article was published: "Arteaga, A. R.A. Pyron, A. Batista, J. Vieira, E. Meneses Pelayo, E.N. Smith, C.L. Barrio Amorós, C. Koch, S. Agne, J.H. Valencia, L. Bustamante & K.J. Harris. 2024. Systematic revision of the Eyelash Palmpitviper Bothriechis schlegelii (Serpentes, Viperidae), with the description of five new species and revalidation of three. Evolutionary Systematics. 8, 15–64."

In it, the species that gives its name to the complex, B. schlegelii, is redescribed based on its holotype and material from its distribution restricted to the central Andes of Colombia. Restricting a species from a wide distribution involves redefining the names that occupy the rest of the distribution. To do this, it is important to review the synonymy of the species in question, and detect previous names that were described for other populations. For example, Steindachner described Bothrops (Teleuraspis) nigroadspesus in 1870, from Central America. Its holotype remains in the Museum of Natural History in Vienna today. As it is the first name assigned to an eyelash viper in Central America, it has the precedence, and therefore, the Central American populations, from southern Mexico to Panama, recovered this name, as Bothriechis nigroadspersus (Steindachner, 1870).

The same occurred with other populations of eyelash vipers, which recovered names immersed in the synonymy of *B. schlegelii*, such as *Bothriechis nitidus* (Günther, 1859) and *B. torvus* (Posada Arango, 1889). The only unchanged species of eyelash viper is *B. supraciliaris*. The remaining populations recognized by molecular and morphological work, which previously fit into the name *B.*

schlegelii, after the new redefinition had no available name and thus, needed to be described as five new species.

Below I present accounts on each of the species as currently understood after Arteaga et al. (2024).

Accounts

Bothriechis schlegelii (Berthold 1846). Schlegel's Eyelash-Pitviper.

It is the type species of the *schlegelii* complex, which keeps the original name but has reduced enormously its distribution. It is now endemic to the Andes of the central and western Cordilleras of Colombia (from Cauca in the south to Antioquia in the north) which is extended over an area of 40,432 km². Its altitudinal distribution is in medium and high mountains, between 1000 and 2600 m. It is a robust species, with males reaching 834 mm and females, 969 mm.

The supraciliary scales of *B. schlegelii* are slightly to moderately prominent. There are two to three of them. The species' chromatic variation is, with that of *nigroadspersus*, the most capricious of all, although the "oropel" phase is not yet known. It is an arboreal



Figure 4. B. schlegelii Quindio, Colombia.





Figure 5. B. schlegelii juvenile, Antioquia, Colombia.

species that lives in low vegetation, and also is often found on the ground. It inhabits primary and secondary cloud forests, crops (coffee) and can even visit gardens in rural areas. Although they are normally docile, they can defend themselves if attacked or disturbed. They usually feed on rodents, small birds and lizards. The species was dedicated to the German zoologist Hermann Schlegel (an "-i" or two at the end of a name in Latin indicates it is a masculine genitive; applied to male persons) by its author Arnold Berthold.

Bothriechis nigroadspersus Steindachner, 1970. Central American Eyelash-Pitviper.

It is the species that currently has the greatest distribution in the complex, covering southern Mexico (Chiapas, Oaxaca); Belize, Guatemala, Honduras, Nicaragua, Costa Rica and Panama, in primary and secondary forests, crops and even gardens, between 0 and 1450 masl. It is characterized by having two long and protruding supraciliary scales, especially in juveniles and males (the former being shorter than the latter). It is probably the species of snake with the greatest variability in its coloration. There are clearly aposematic specimens (yellow, white, pink, orange) as well as very cryptic (with a lichen or mossy pattern) ones. The famous yellow phase (oropel) is one of the most characteristic, and can make up to 60% of the total number in some populations. The holotype of *B. nigroadspersus* is yellow with scattered black spots (hence its Latin name, which means, sprinkled with black little spots). It reaches a measurement of up to 626 mm (25.6 in) for males and 916 mm (36.06 in) for females. It is normally found in diverse vegetation (from 30 cm to several meters high) ambushing its prey of lizards, frogs, birds and mammals.

Bothriechis supraciliaris Taylor, 1954. **Blotched Eyelash-Pitviper.**

This is the second species of eyelash viper present in Central America, although its distribution is much smaller than that of B. nigroadspersus. It is located on the Pacific slope of the Talamanca Mountain Range in Costa Rica and adjacent Panama (Provinces of San José, Puntarenas and Chiriquí), in medium mountain areas between 700 and 1700 m altitude, covering about 3,568 km².



Figure 6. B. nigroadspersus Costa Rica; note that "nigroadspersus" means sprinckled with black, although not all individuals bear this character.



Figure 7. B. supraciliaris from Costa Rica.

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Figure 8. B. torvus from Chocoan Colombia (photo by Jose Vieira).

Although it is extremely similar to the previous one and has a wide chromatic variation, it is best distinguished (in addition to the biogeographic region it occupies, where no cases of sympatry with B. nigroadspersus are known) by the arrangement of the dorsal spots (connected= nigroadspersus; not connected= supraciliaris). It also has two or three raised supraciliary scales, hence its specific name in Latin (supra= above; cilium= evelashes; -is= suffix that denotes belonging). The maximum measurements recorded are 382 mm for males, and 583 mm for females, although I have observed many specimens in collections that exceed these sizes, approaching the biggest sizes seen in *B. nigroadspersus*. Its behavior and prey are similar to those of the previous species.

Bothriechis torvus (Posada-Arango, 1859). Birri Eyelash-pitviper.

This Chocoan eyelash viper was described by the doctor Andrés Posada-Arango in 1859 as *Thanatophis torvus*. It has three rounded supraciliary scales of moderate size. Males reach 378 mm (14.88)

in), while females can reach 657 mm (25.86 in). They are distributed throughout areas of primary and secondary forest in the Darien region of Panama, the Colombian Chocó and parts of the Magdalena River Valley, covering 61,466 km² in an altitudinal range between 60 and 1450 m. Their coloring patterns are quite variable, but there is still a long way to go to quantify them. It is not known to have a yellow (oropel) phase. The adjective "torvus" in Latin means "fierce looking."

Bothriechis nitidus (Günther, 1859). Ecuadorian Eyelash-Pitviper.

The image accompanying Gūnther's original description is simply beautiful. One of the most distinctive eyelash species is the green viper that is found throughout western Ecuador, where it is endemic to a region spanning 37,400 km². From the cloud forests of Mindo to the low areas of Choco (from 0 to 2230 m), this viper is found in areas of forests with little or no intervention. Of robust conformation, males reach 60 cm (23.62 in) while females reach 86 cm (33.85 in). The most



Figure 9. B. torvus
Darien, Panama
(photo by Abel
Batista).

common coloration is green, with various patterns, including that of its holotype made up of transverse red stripes; but there are also animals with a lot of black or pink. No oropel phase (yellow) is known in this species. Its supraciliary scales can be almost negligible, perhaps somewhat prominent in youngsters and males. Their behavior and prey are similar to those of previous species. The meaning of "nitidus" in Latin is: elegant or brilliant, in reference to his beautiful and peculiar attire.

Bothriechis khwargi Arteaga, Pyron,
Batista, Vieira, Meneses-Pelayo, Smith, Barrio-Amorós, Koch, Agne, Valencia, Bustamante & Harris, 2024. Khwarg's Eyelash-Pitviper. This species, along with B. rahimi, is the smallest of the schlegelii complex with males known to be up to just 219 mm (8.62 in), and females up to 610 mm (24.01 in). However, it is possible to find larger individuals. This species has two supraciliary scales that are triangular but low. There are few coloration patterns described, but the "oropel" phase is not known. Bothriechis khwargi is distributed on the western slope of the Eastern Cordillera of Colombia, between

Figure 10. Another *B. torvus* Darien, Panama (photo by Abel Batista).



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Figure 11. B. nitidus from Western Ecuador (photo by Jose Vieira).

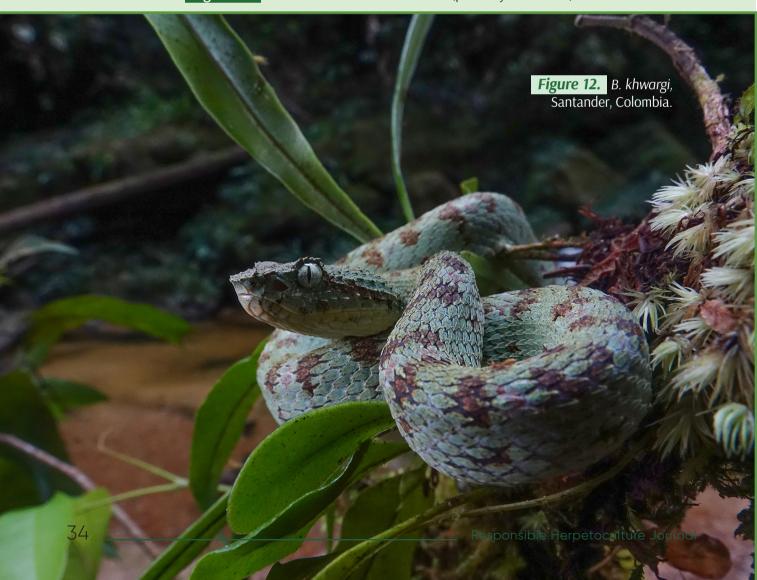




Figure 13. B. klebbai juvenile (photo by Elson Meneses).

167 and 1800 m of altitude, extending over 14,697 km², and is endemic to this country. Habits and feeding unknown but probably similar to other species in the complex. This

species is named in honor of Dr. Juewon Khwarg, in recognition of his support of the discovery and protection of new species of vipers in the Andes of Colombia.



Figure 14. B. rahimi, oropel phase, Western Ecuador.



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Bothriechis klebbai Arteaga, Pyron, Batista, Vieira, Meneses-Pelayo, Smith, Barrio-Amorós, Koch, Agne, Valencia, Bustamante & Harris, 2024. Klebba's Eyelash-Pitviper.

A robust viper, where males reach 671 mm (26.41 in) and females reach 874 mm (34.41 in), with low and granular supraciliary scales, sometimes pointed. There are few coloration patterns described, but the yellow phase is not known. It is a species only inhabiting cloud forests of the Cordillera Oriental of Colombia, between 1418 and 2380 m, occupying a total of about 20,100 km². Habits and feeding are unknown but probably similar to all species in the complex. Named after Casey Klebba, whose dedication to the preservation of tropical biodiversity is exemplary.

Bothriechis rahimi Arteaga, Pyron, Batista, Vieira, Meneses-Pelayo, Smith, Barrio-Amorós, Koch, Agne, Valencia, Bustamante & Harris, 2024. Rahim's Eyelash-Pitviper.

This is the South American species most similar to *B. nigroadspersus*, due to its three protruding and pointed supraciliary scales. It is a graceful and delicate species that only reaches 336 mm (13.22 in) in males and 494 mm (19.44 in) in females (which does not mean that larger individuals do not exist). Various

colorations exist, including "oropel". It inhabits the northwestern Chocó of Ecuador and adjacent Colombia, occupying about 6000 km² of low Chocó areas, between 10 and 200 m altitude. The specific epithet "rahimi" is a patronym honoring Prince Rahim Aga Khan, a firm inspirational environmentalist.

Bothriechis rasikusumorum Arteaga, Pyron, Batista, Vieira, Meneses-Pelayo, Smith, Barrio-Amorós, Koch, Agne, Valencia, Bustamante & Harris, 2024. Shah's Eyelash- Pitviper.

An eyelash viper with low or moderately pointed supraciliary scales, of medium size, males up to 65 cm (25.59 in), females up to 80 cm (31.49 in). It lives in the Eastern Cordillera of Colombia basically in the department of Huila, on both slopes of the upper Magdalena River, between 1,298-2,180 m, occupying 6,578 km², being the only species that barely penetrates into the Amazon bioregion, although this distribution must be due to a recent expansion event. Habits and feeding are unknown but probably similar to all species in the complex. The specific epithet "rasikusumorum" is a patronym (in genitive plural, ending in -orum) honoring Rasik Shah and Kusum Shah, who helped fund expeditions leading to the discovery of this species.

Bothriechis hussaini Arteaga, Pyron, Batista, Vieira, Meneses-Pelayo, Smith, Barrio-Amorós, Koch, Agne, Valencia, Bustamante & Harris, 2024. Hussain's Eyelash-Pitviper.

The last viper is the southernmost form, known from southwestern Ecuador and northwesternmost Peru (just a tiny portion in the Tumbes region), totaling 13591 km², from 1-1680 m a.s.l. It is a medium sized eyelash viper, with males reaching 608 mm (23.93 in) and females 656 mm (25.82 in), with low granular to triangular supraciliary scales. Some variants have a reddish coloration unique to the complex, although there are also black-green, pink and even "oropel" morphs. The specific epithet "hussaini" is a patronym honoring Prince Hussain Aga Khan, who has dedicated his life, influence, and wealth to environmental conservation.

Venom

All these vipers are, of course, venomous. But the venom varies from quite toxic in *B. nigroadspersus*, to less edematous, hemorrhagic and lethal in all the South American species. The venom of *B. nigroadspersus* is hemotoxic and strongly myonecrotic compared to other Central American vipers. In humans, it causes intense localized pain, progressive hemorrhagic edema,

and, in some cases, hemorrhagic blisters or hives, ecchymoses, and necrosis, causing death in 3-6 cases every year. This data is from the sixties and seventies, and nowadays, probably the number of deaths is 0. In *B. supraciliaris* the venom has a potent hemorrhagic action, moderate myotoxicity, and very weak procoagulant activity. Most bites of *B. schlegelii*, *B. rahimi*, *B. torvus* and *B. nitidus* have been successfully treated with polyvalent antivenom. The venom of *B. khwargi*, *B. klebbai* and *B. rasikusumorum* have not yet been studied.

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I deeply want to thank Alejandro Arteaga and the rest of colleagues and coauthors of the paper for such good times in the wild searching for those amazing complex of vipers. We shared many nice talks in remote forests of the last remaining Neotropical wilderness, as well as in European Museums, leading to the conclusion of the paper by Arteaga et al (2024), that I have aimed to explain in a more accessible format.

I would also like to thank Alejandro Arteaga, Jose Vieira, Abel Batista and Elson Meneses Pelayo for allowing me to use some of their amazing photos exclusively for this article.

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