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Article

Description of the Northern Green Anaconda (*Eunectes akayima* sp. nov. Serpentes; Boidae): What Is in a Name? †

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LSID: urn:lsid:zoobank.org:act:004D5E05-D3D5-4685-BC7D-E82088E31FCD.

Abstract: While elucidating the evolutionary trajectory of green anacondas, we previously documented the existence of two distinct species, *Eunectes akayima* sp. nov. and *Eunectes murinus* (Linnaeus, 1758), that separated approximately 10 million years ago. Our research integrates a novel molecular clock approach, focuses on tectonic plate movements with fossil records as minimal chronological markers, and offers a refined understanding of speciation events in relation to major biogeographical occurrences in South America. Mitochondrial DNA analysis demonstrates a significant genetic divergence between the species, which is supported by a notable difference in sexual size dimorphism (SSD) intensity between the two species, along with other morphological differences. This paper also rectifies earlier oversights in the description of the new species and clarifies taxonomic ambiguities in compliance with the International Code of Zoological Nomenclature (henceforth ICZN). In addition, we designate a neotype for *E. murinus* to stabilize the group. In an effort to honor Indigenous nations, *E. akayima* sp. nov. derives its name from the Carib language, advocating for the inclusion of traditional names in scientific discourse. Our paper not only contributes to the taxonomic stability of anacondas but also advocates for the usage of Indigenous names in zoological nomenclature by adopting a more inclusive and flexible approach to the ICZN and eliminating unintended exclusionary practices that we have inherited in science as in other disciplines.

Keywords: cryptic diversity; Boidae; South America; Llanos; Pebas system; Orinoco basin; redundant species

Citation: Rivas, J.A.; Terra, J.S.; Roosen, M.; Champagne, P.S.; Leite-Pitman, R.; De La Quintana, P.; Mancuso, M.; Pacheco, L.F.; Burghardt, G.M.; Vonk, F.J.; et al. Description of the Northern Green Anaconda (*Eunectes akayima* sp. nov. Serpentes; Boidae): What Is in a Name? *Diversity* **2024**, *16*, 418. https://doi.org/10.3390/d16070418

Academic Editors: Michael Wink, Manuel Elias-Gutierrez and Jessica Frigerio

Received: 20 May 2024
Revised: 6 July 2024
Accepted: 9 July 2024
Published: 18 July 2024

1. Introduction

Our recent paper [1] described a new species of green anaconda that had been hidden in plain sight due to its largely cryptic nature. That paper presented data on the genetic divergence between the Northern Green Anaconda, *Eunectes akayima* sp. nov., and the Southern Green Anaconda, *Eunectes murinus* (Linnaeus, 1758), which indicated that the species split approximately 10 mya. This made green anacondas a particular example of diversification of sister taxa between, roughly, the Amazon Basin and the Orinoco Basin [1]).

Our paper aimed to comprehensively understand the evolution of the genus *Eunectes* Wagler, 1830 in the paleo-geographical background where it occurred. We implemented a molecular clock analysis featuring tectonic plate knowledge using fossils only as hard minima for the taxa. This differs from other approaches that are either based solely on fossils or that treat fossils as hard maxima. We used our approach because both the odds of fossilization occurring, as well as fossils being found, are low. So, a fossil may be found for the first time in a stratum that is many million years younger than the species. This problem is especially acute in areas like South America where large areas of the continent were covered by acidic black water swamps [2–6]. In these habitats, bones would have dissolved before fossilization took place. Our choice of the clock seems successful, as it places splits of different lineages at times coincident with major biogeographical events that could have explained diversification. As such, it placed the separation of *Eunectes* from its sister genus *Epicrates* (Linnaeus 1758) at 46–35 mya, a time when flooding conditions started in the continent due to the damming of the proto-Orinoco/-Amazon River. It makes sense that the availability of aquatic habitat was linked to the appearance of not only *Eunectes* as an aquatic lineage but also other aquatic lineages on the continent [1,6]. The diversification within *Eunectes* into an *E. akayima* sp. nov./*E. murinus* clade and *E. notaeus* Cope, 1862 occurred at the peak of flooding in the continent, about 24 mya, during the formation of the Pebas system, which was a mega wetland that occupied all of the western parts of the continent between 24 and 10 mya [3,4]. It also makes sense that *Eunectes*, an aquatic lineage, would have diversified then as more and more diverse aquatic habitats became available. Lastly, the split between *E. akayima* sp. nov. and *E. murinus* coincides with the formation of a paleo-arch (the Vaupés arch) resulting from the rise of the Andes, which created a ridge splitting the northern and southern parts of South America. This must have acted as a vicariant barrier producing allopatric speciation of these two species. Taken together, this shows that our choice of molecular clock was not only technically sound, but it was also useful to help reconstruct the evolution of *Eunectes* in the context of the paleo-history of South America, which was our main goal.

Our analysis was based only on mitochondrial DNA (mDNA) since the nuclear genes we explored did not have the variation needed to detect the differences. However, the divergence of the mDNA between both lineages is 5.5%, which is enough to support the separation of two different species. This is corroborated by other recent studies on vertebrate taxa [7,8]. In addition, we are unaware of any instance in which a mDNA divergence of this magnitude was found not to be a legitimate difference between the two species. We are also not aware of any lineage being separated for 10 my and still remaining the same species, with the exception of fossil species for which the DNA can no longer be sequenced to test for molecular divergence. This, along with new morphological evidence found presented in the current paper, supports the conclusions made in [1], that the green anaconda complex diverged into two species. A recent editorial statement [9] expressed skepticism about our results but they did not present any new data supporting their claim.

The aim of our paper was originally to obtain a better understanding of the evolution of the *Eunectes* complex. However, in the process of doing so, we found considerable evidence for the existence of a new species, which we described. We acknowledge some mistakes were made in this description, especially regarding the application of ICZN [10]. There are aspects of the nomenclature and taxonomy of both *E. akayima* sp. nov. and *E. murinus* that require more clarification.

In this contribution, we correct the mistakes made in the original paper as noted by other authors [9,11] and clarify some issues that could have been more explicit. Nonetheless, we stand by the scientific merit and conclusions of our paper. Here, we formally describe *Eunectes akayima* sp. nov., as the description in Rivas et al. [1] was not as clear as it should have been to comply with Article 13.1.1 of the ICZN. In order to stabilize the nomenclature of all green anacondas, we also propose a neotype for *E. murinus* that has been sequenced and has available tissue. Lastly, we use data from the literature [12–19], from sites in Peru and Brazil and museum collections, to document morphological differences between *E. akayima* sp. nov. and *E. murinus* that were not recognized in the original paper. Since some specimens were measured live (measured three times and averaged for accuracy) [12] while others were measured preserved, or as dried skin, we compared measurements within the same categories (i.e., live animals with live animals, preserved animals with preserved animals) unless otherwise specified. Data used in tables and figures is available as supplemental material.

2. A General Discussion of the Nomenclature

2.1. *Eunectes akayima* sp. nov.

The specific epithet we used, *akayima,* means "The Great Snake" in the Carib language; a group of Indigenous people who lived in the northern part of South America that contains most of the distribution of the species [1]). In our paper, we argued that since the Indigenous people have been using this name for hundreds of years, *akayima* should be the specific epithet and may be considered a senior synonym. Admittedly, this was an unorthodox position since the ICZN only accepts names that have been published in scientific (Western) literature as valid. We want to stress that *E. akayima* sp. nov. is valid in any case, as none of the currently available names within *Eunectes* fit the new species (see below).

2.2. *Previous Names for Green Anacondas*

While other synonyms have been used for anacondas over the years, some mentioned by McDiarmid et al. [20] and all those listed by Dubois et al. [9], most of the type specimens were collected (or bought from vendors) around what is currently Suriname and French Guiana, where both species may coexist.

An exception from this pattern is *Eunectes barbouri* Dunn & Conant, 1936, which is a current synonym of *E. murinus* and comes from the Island of Mara-jó in Pará state, Brazil. We believe that the source of origin of a specimen is poor criterium to identify a species in places where sampling is spotty [1] as is the case with *Eunectes*, but when the distance of a specimen from the closest known location is substantial, the place of origin can still be a valid criterium. Throughout our sampling, we did not identify any *E. akayima* sp. nov. anywhere close to Pará State so the place of origin would suggest that it is not *E. akayima* sp. nov. [1]. In addition, reading the description of *E. barbouri* [17] on page 504, after saying that it was a live male being held in at Philadelphia Zoo, it reads as follows:

"Measurements: Total length 4051 mm.; tail length 610 mm".

As we have measured in excess of 1400 anacondas of all sizes, this immediately shows us that it cannot be *E. akayima* sp. nov. Although it was only recently recognized to be a new species, *E. akayima* sp. nov. is the most studied anaconda in the world, and its reproductive biology is well known [12,15,21,22]. It has a very strong SSD, among the strongest found in terrestrial vertebrates, with males being much smaller than females [15,23]. In a study involving 821 wild captures (including more than 400 males), the average length of the males was 237 cm (SD 50.3). They seldom exceed 3 m in total length, and none exceed 3.4 m [12]. The length of the specimen of *E. barbouri* alone is enough to rule it out as being conspecific with *E. akayima* sp. nov. because males of the latter species do not reach these sizes. On the other hand, males of *E. murinus* are known to grow very long, even larger than the type of *E. barbouri* (Figure 1, Table 1). Therefore, we hereby synonymize *E. barbouri* with *E. murinus sensu* Rivas et al. [1].

Figure 1. A large male of *E. murinus* found in Las Piedras River, Las Piedras Amazon Center, Peru. TL: 452.8, SVL 401.7. M = 41 kg. This specimen is about 50% larger than males of *E. akayima* sp. nov. that have been recorded. It is striking how slender this animal is for this size, which corresponds with the morphology normally found in males [16]. (Photo Jaroen Ten Haaf.)

Table 1. Comparison of total size (cm) between adult *E. murinus* and *E. akayima* sp. nov. SD = standard deviation, N = sample size, Min = minimum value, Max = maximum value, LCI = lower 95% confidence interval, UCI = upper 95% confidence interval for total length. Data from *E. akayima* sp. nov. are from [16], and data from *E. murinus* are from [13,14,19]). CV is coefficient of variation that is calculated by dividing standard deviation by mean [24]. For total length data (but not CV calculations), we combined data from museum and live specimens.

	Mean	**SD**	**N**	**Min**	**Max**	**CV**	**LCI**	**UCI**
E akayima female sp. nov.	341.88	74.31	272.00	242.67	630.00	0.2174	333.05	350.71
E. akayima male sp. nov.	253.43	31.88	353.00	188.25	333.67	0.1258	250.10	256.75
E. murinus female	389.56	93.19	39.00	241.10	632.00	0.2392	359.35	419.77
E.murinus male	276.23	61.65	66.00	188.00	487.00	0.2232	261.07	291.38

Other synonyms include *Boa gigas* Latreille in Sonnini and Latreille, 1802 [25], *Boa anacondo* Daudin, 1803, and *Boa aquatica* Wied-Neuwied, 1823. Since there is no type specimen for these synonyms, and, given that they all come from areas where both species may coexist, there is no way of knowing to which of the two species they belong. Therefore, we consider these taxa as *nomina dubia* and deem them unusable for the taxonomy of *Eunectes.* As these taxa have only been used as synonyms for most of their history, this position does not cause unnecessary nomenclatural instability. Aside from this, Dubois et al. [9] mention in paragraph 7.2 that they consider *Boa gigas*, *Boa anacondo*, and *Boa aquatica* to be based on representatives of the 'southern lineage' *sensu* Rivas et al. [1]; under this logic these names would be junior synonyms of *E. murinus.* In addition, we follow Dubois et al. [9] in their opinion that *Boa scytale* Linnaeus 1758 is likely based on species of *Erythrolamprus* Boie, 1826 and *Homoroselaps* Jan, 1858 and by that not available for a species of anaconda.

Another name that has been used for anacondas is *Boa aboma* Daudin, 1803. This name referred to various specimens now lost and has been considered a synonym of *Boa murina* for most of its history [9,26]. Dubois et al. [9] believe that the newly identified species of anacondas, *E. akayima* sp. nov., should be named *Eunectes aboma* because the lectotype of *Boa aboma* was found in "...a precise locality, now situated in Guyana" (p:37). However, this is an uncharacteristic mistake of these authors. In their Table 1, they correctly place the source of this specimen in Suriname (p: 24). Furthermore, the type specimen was described in a book about an expedition to Suriname [27]. On page 170, it says that the snake was found "between Cormoetibo and Barbacoeba". After page 30* of this book, there is a foldout map that shows this location in the Cottica River (Figure 2). The location is near the village of Cassipore (coordinates: Lat 5.77, Long −54.36) which can be found around the section where the Cottica River veers west (Figure 2). This location is to the Southeast of Paramaribo, about 40 km from the border with French Guiana, a known contact zone between *E. akayima* sp. nov. and *E. murinus* [1]. Thus, if further evidence is absent, this nomen should be considered a nomen dubium because there is no way of knowing to which species it belongs to based on the type locality alone. However, looking at the description of the specimen, it is possible to identify it as *E. murinus*. Stedman ([27], p. 175) described the snake:

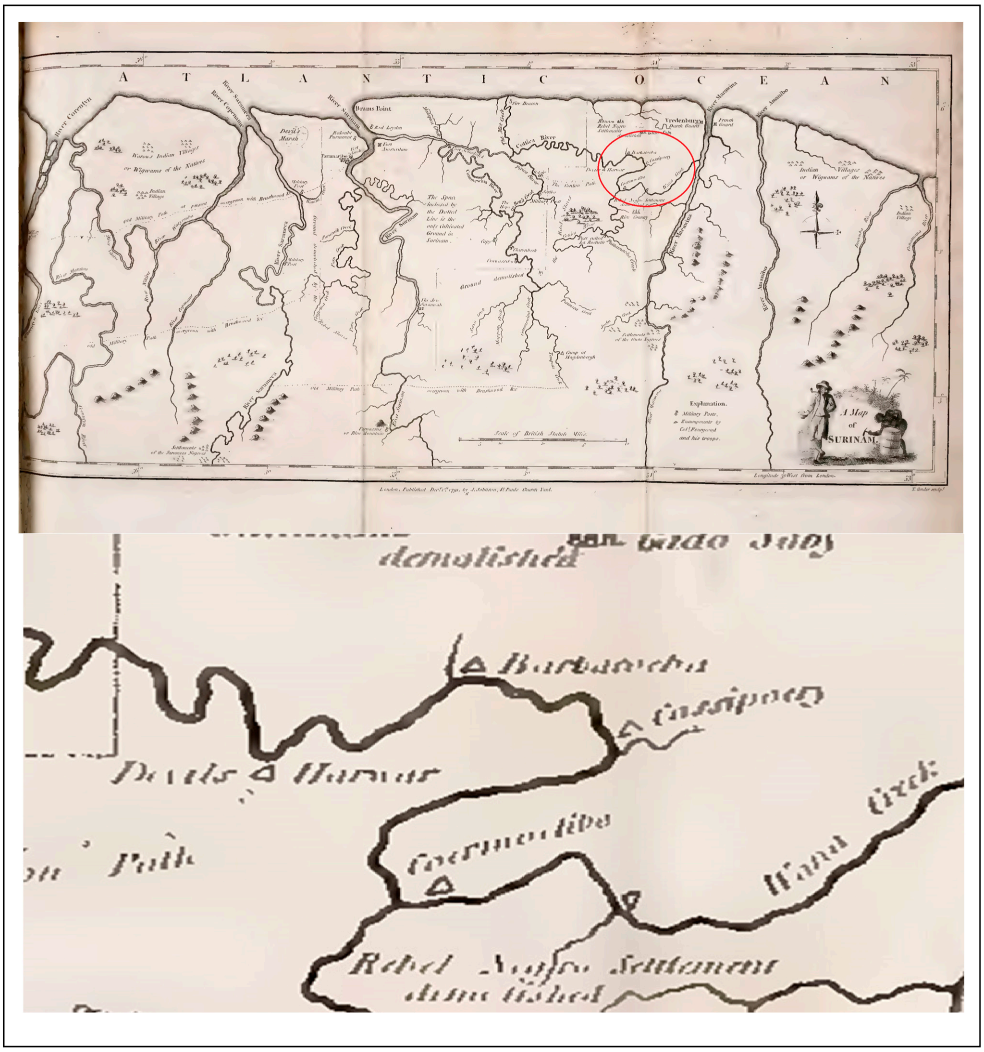

Figure 2. A map from Suriname from Stedman [27] after page 30*. It shows where *Boa aboma* was found and killed. The upper figure shows the locality in a red circle for reference within the country. The river on the east side touching the red circle is the boundary between Suriname and French Guiana. The lower figure shows the amplified area contained in the circle and shows the precise stretch of the Cottica River between Cormoetibo and Barbacoeba where the snake was found.

"Its head is broad and flat, small in proportion to the body, with a large mouth, and a double row of teeth: it has two bright prominent eyes; is covered all over with scales, some about the size of a shilling; and under the body, near the tail, armed **with two strong claws like cock-spurs**, to help it in seizing its prey" (emphasis added).

Here again, familiarity with anacondas makes a difference. Female anacondas have very small and inconspicuous spurs in comparison to males (Figure 3 [15]). The size of these spurs, described as comparable to those of a rooster, can only be found in a male anaconda, and a very large one at that. A 6-meter-long female would have spurs 8.8 mm long, while a male of the same size would have spurs of 17.5 mm [15], which is more on par with the size of a rooster's spurs. As explained above, *E. akayima* sp. nov. is strongly sexually dimorphic, with males never reaching a length anywhere close to that size. Therefore, we hereby synonymize *Boa aboma* with *E. murinus sensu* Rivas et al. [1]

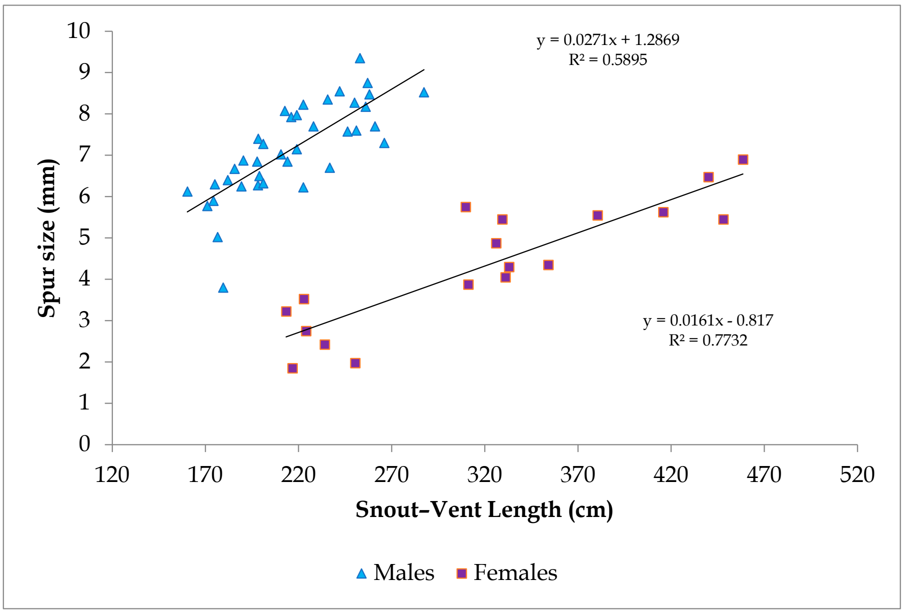

Figure 3. Spur size of *E. akayima* sp. nov. in relation to snout–vent length. Data from [15].

2.3. The True Identity of *E. murinus* (Linnaeus 1758)

Linnaeus based his description on at least one specimen presumably in his collection and the specimens from three drawings: two from Seba's Catalog [28] and one from Physica Sacra [29]. Because the origin of these specimens is just "America", there is no way of knowing which species he described based on the source of origin. At the time, most specimens came from the Suriname and French Guiana region and both species have been identified in that area. In our original paper, we assigned the new species to the northern clade because the core distribution of the species is limited to the Orinoco Basin, even if it may be found in neighboring watersheds, and European explorers did not arrive at the Orinoco Basin until later. Another reason we chose the northern clade as the new species is because it has a smaller distribution. Leaving *E. murinus* as the one with a larger distribution would lead to less nomenclature instability. We still believe these are legitimate criteria, but now that morphological differences have been identified, we can more confidently ascertain that at least some of the snakes Linnaeus described are *E. murinus sensu* Rivas et al. [1].

While most type specimens of *Boa murina* are considered lost to date [9,30], in his catalog of Linnean type specimens, Andersson [31] describes the Linnean type specimens for *Boa murina*. This specimen is 930 mm in total length with a tail of 100 mm. So, dividing the tail length by SVL (100/830), we obtain 0.1205 which is well within the range of a female *E. murinus sensu* Rivas et al. [1] and outside the 95% CI *E. akayima* sp. nov. (Table 2). Based on this observation, this confirms that at least part of the syntypes of *Boa murina* are indeed *E. murinus sensu* Rivas et al. [1].

Table 2. Comparison of relative tail length (tail/SVL) between adult *E. murinus* and *E. akayima* sp. nov. SD = standard deviation, N = sample size, Min = minimum value, Max = maximum value, LCI = lower 95% confidence interval, UCI = upper 95% confidence interval for total length. CV is coefficient of variation that is calculated by dividing standard deviation by mean. Data from *E. akayima* sp. nov. are from [16], and data from *E. murinus* are from [13,14].

	Mean	SD	N	Min	Max	CV	LCI	UCI
E akayima sp. nov. female	0.139	0.0108	78	0.1107	0.1660	0.0777	0.1364	0.1412
E. murinus female	0.118	0.0179	22	0.0908	0.1520	0.1512	0.1102	0.1261
E. akayima sp. nov. male	0.173	0.0127	104	0.1314	0.2215	0.0736	0.1706	0.1755
E. murinus male	0.176	0.0128	11	0.1488	0.1886	0.0728	0.1671	0.1842

2.4. E. murinus sensu Rivas et al. [1]

To provide a stable definition of *E. murinus* for comparison with the new species, Rivas et al. [1] mistakenly designated a lectotype for *E. murinus* from a contemporary sample that they had genotyped. Clearly, this lectotype did not meet the requirements of Article 75 of the Code [10] as it was not a specimen from the original type series. What is really needed is a neotype, a specimen from the same species that has well-preserved DNA, so it can be used to differentiate the species. Designating a neotype under the Code can be a simple matter if there is no existing type specimen. If there is a type specimen available or if there is confusion about the identity of the species, the Commission for International Zoological Nomenclature needs to make a ruling. Unfortunately, the case of *E. murinus* has previously left confusion as to whether syntypes of this species are still in existence and there are hints that multiple species were mixed in the syntype lot.

Although the provenance of the specimen is uncertain in the archives of the Swedish Museum of Natural History, Stockholm, Sweden, specimen NRM 9, which is clearly an anaconda, has been accepted by some as a possible syntype of *Boa murina.* In some cases, it was mistakenly referred to as the holotype [20,32]. However, Dubois et al. [9] discuss this matter and express some doubts on the syntype status of this specimen. The scale count of NRM 9 does not match the one cited by Linnaeus. They argue that if Linnaeus did not use its scale counts in the diagnosis of this species it might not be a valid specimen of the syntype series.

However, the scale count is not the only problem. The main evidence that NRM 9 was not the specimen used to describe *Boa murina* is that NRM 9 is, in fact, an anaconda. There is evidence in the description that the primary syntype described by Linnaeus was not an anaconda. Linnaeus [33] writes "*Corpus bipedale*" or "the body is two feet long". Here again, being very familiar with the species makes a big difference. As we have measured upwards of 600 neonates from more than 30 females, this statement immediately makes us suspect that it might not be an anaconda. Anacondas are born at 68.42 cm SVL (SD 4.01) [12]. The probability that a neonate is two feet long in SVL falls far outside the 95% confidence interval. Neonate anacondas are exceedingly difficult to find because of their small size and crypsis. In a study involving 821 field captures, only 25 (3%) were neonates [34]. The combined probability is so small that we have to consider that it might not have been an anaconda. In addition, the color description is "*Color glaucus*" or grey color or gleaming grayish. This does not describe the color of anacondas, or even NRM 9 after 250+ years of preservation for that matter. Furthermore, in the 1758 version of Systema Naturae, Linnaeus [35] writes: "*Rufus maculis supra rotundatis*" which translates as "round red spots on top". This is another description that does not match the likeness of anacondas or of NRM 9. They have red stripes, not red spots; and they are only on the head. Last, Linnaeus talks about the eye being on a line (*Caput pone oculus linea longitudinali*) which *Eunectes, Epicrates, and Boas* have. However, he does not mention that the eyes are superior. Not many snakes have superior eyes and nostrils, and Linnaeus might have not seen many (any?) with that eye feature. But in the description of the eye, he mentions something common with other boas and not what makes it exceptional.

We have to consider that the snake he was describing did not have superior eyes. Taken together, this tells us that the specimen that Linnaeus examined, in all likelihood, was not an anaconda. We may never know for sure what species it was that Linnaeus was describing, but what is clear is that it was not NRM Lin.9. Neither does its scale count, size, or color match Linnaeus's description. On the other hand, other syntypes, like the specimens depicted on plates 23 and 29 of Seba [28], as well as the one depicted on plate 606 of Physical Sacra [29], are clearly identifiable as anacondas (Figure 4). All these specimens are considered lost [30], but Seba's specimen from plate 29, labeled ONID Sm 2, was validly proposed as a lectotype for *E. murinus* "*in absentia*" by Dubois et al. [9] to fix the name on a species of anaconda, as long as no proper neotype is designated. This lectotype designation also changes the status of all other onymophoronts from (possible) syntype to paralectotype, removing their name-bearing status and paving the way to assign a neotype that is more likely to preserve nomenclatural stability. So even if NRM 9 turns out to be a primary syntype used by Linnaeus, which likely can never be proven beyond doubt, it can be set aside now in favor of another specimen that can still be sequenced and has more precise locality data attached to it [9].

To stabilize the definition of *E. murinus*, we hereby deliberately designate MPEG 27,428 from Museu Paraense Emílio Goeldi, Belém, Brazil, as a neotype for *E. murinus*. The specimen is a female that was collected in Altamira, State of Para, Brazil (3°9′16″ S, 52°14′11″ W), October 2011, leg. Emil Hernández, from which we obtained sequence data, with the following accession numbers: Cytb = PP273586, ND2 = PP334818, and ND4 = PP334875. This neotype is needed to confine a more precise type locality, which is currently 'Americas', and to establish a specific identity as the lost specimen of the Seba collection cannot be identified as one of the two known clades (ICZN Article 75.3.1). Single specimens of green anaconda can only be identified at the species level by sequencing and comparing their DNA, a procedure that cannot be conducted on the lost lectotype (ICZN Article 75.3.2). The collection number, collection locality, collection date, and collector make the neotype easy to find in the MPEG collection (ICZN Article 75.3.3). The lectotype is considered lost after Bauer et al. [30] and Rivas et al. [1] did every reasonable efforts to locate the lectotype in European museums and collections but were unable to trace the specimen (ICZN Article 75.3.4). Like the specimen shown on Seba's plate, the newly proposed neotype is a green anaconda. By that, the neotype is consistent with all that is known of the lost lectotype (ICZN Article 75.3.5). As also outlined in [1], the area of origin of the type material described by Linnaeus is unclear, but the neotype is from an area known to be accessed by zoologists in the 1700s in an area where we know *Eunectes murinus* in its current definition occurs. Thus, it is "as nearly as practicable" to the true type locality, as required by Article 75.3.6 of the ICZN [10]. The neotype is currently stored in the publicly accessible collection of the Museu Paraense Emílio Goeldi in Belém, Brazil (ICZN Article 75.3.7). We realize that if the specimen used for the drawing of Seba's plate 29, the lectotype, were to be found, in the future, this neotype would lose its status, but, in the meantime, it grants necessary stability to the nomen. However, Bauer et al. [30] showed that Seba's specimen is unlikely to be recovered.

Molecular diagnostic characters used to identify *E. murinus* include the following autapomorphies for *E. murinus*: T, T, T, C, T, G, A, G, G, and T in Cytb at corresponding nucleotide positions of 132, 133, 156, 159, 213, 219, 378, 420, 447, and 498 (Table 3). Position numbers refer to aligned sequence gene sets (GenBank accession #s in Table S1 of Rivas et al. [1]). A summary of all molecular diagnostic characters for *E. murinus* is detailed in Table 3. Meristic information on this specimen and comparison with a holotype and a paratype of *E. akayima* sp. nov. are presented in Table 4.

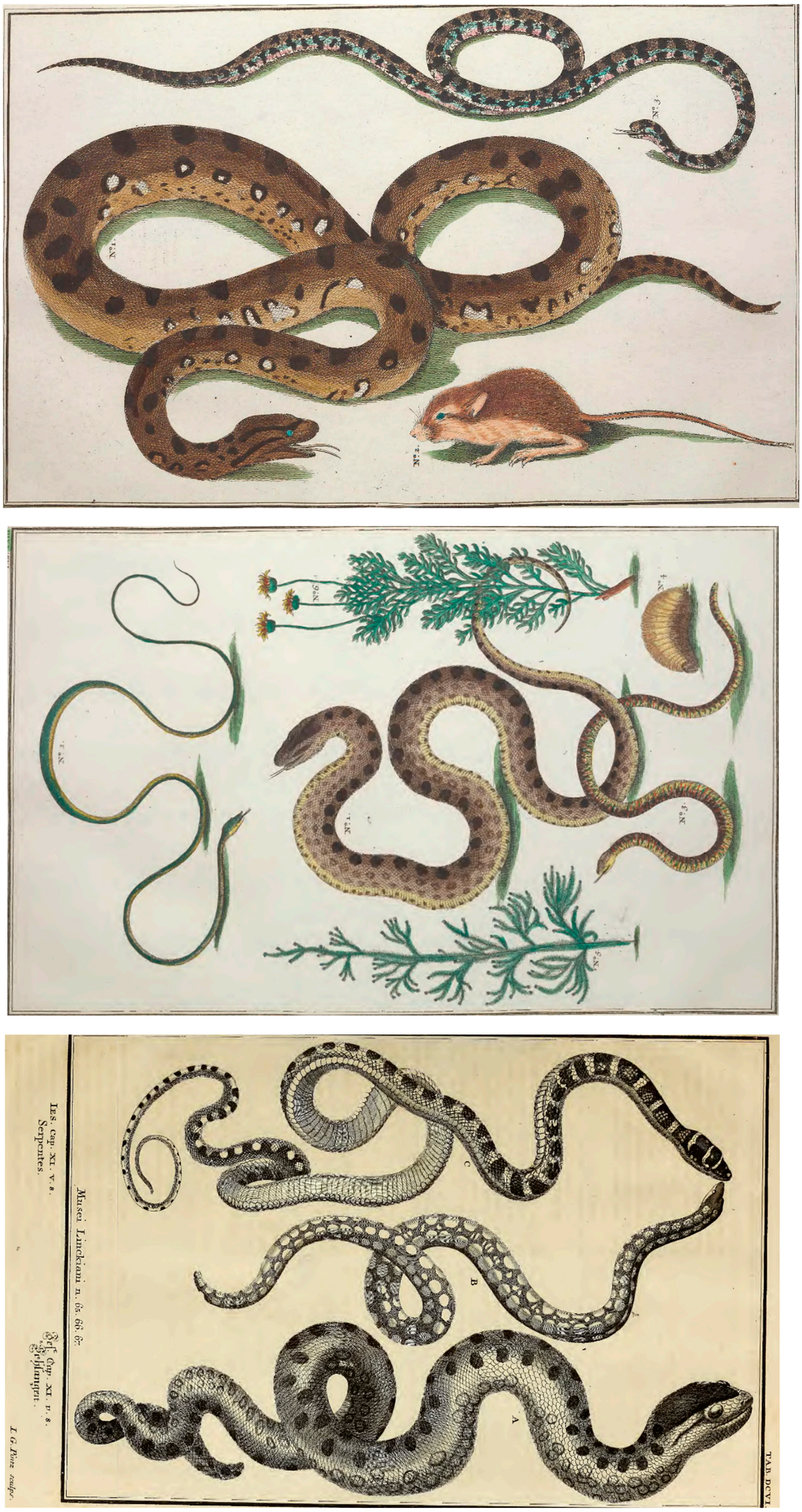

Figure 4. The original syntypes of *Boa murina*. Above: plate 29 of Seba's catalog. Number 1 is a syntype and the specimen that was named as a lectotype of *E. murinus* by Dubois et al. [9]. Middle: plate 23 of Seba's catalog depicting an anaconda in number 1 [28]. Below: plate 606 of Physica Sacra [29] shows the other syntype labeled A.

Table 3. Molecular diagnostic characters distinguishing *Eunectes akayima* sp. nov. from *E. murinus*. Nucleotide base position 1 refers to the aligned gene sequence set available in GenBank, which corresponds with the following mitochondrial genome positions: Cytochrome b alignment position 1 corresponds with position 15,364 of the *E. notaeus* mitochondrial genome (accession # AM236347). The NADH 2 alignment position 1 corresponds with position 5193 of the *E. notaeus* mitochondrial genome (accession # AM236347). The NADH 4 alignment position 1 corresponds with position 12,081 of the *E. notaeus* mitochondrial genome (accession # AM236347). The molecular diagnostic characters reported did not have any intraspecific divergence at each of the positions noted. The numbers in parentheses following each species name indicate the number of specimens that were included in the sequence analysis.

Cyt b					
Position	***E. akayima* sp. nov. (22)**	***E. murinus* (25)**	***E. beniensis* (7)**	***E. deschauenseei* (4)**	***E. notaeus* (8)**
15	A	A	G	G	G
42	A	A	A	G	A
45	G	A	A	A	A
63	G	G	A	A	A
64	C	C	A	A	A
78	C	C	T	T	T
93	T	T	A	A	A
96	A	G	C	C	C
102	C	C	T	T	T
108	A	A	G	A	A
117	T	C	C	C	C
132	C	T	C	C	C
133	C	T	C	C	C
156	C	T	C	C	C
159	T	C	T	T	T
177	T	C	C	C	C
213	C	T	C	C	C
219	A	G	A	A	A
258	G	A	A	A	A
273	T	C	C	C	C
305	T	C	C	C	C
307	T	C	C	C	C
339	C	T	T	T	T
345	T	T	C	C	C
378	C	A	C	C	C
420	A	G	A	A	A
444	T	C	C	C	C
447	A	G	A	A	A
498	C	T	C	C	C
501	C	T	C	C	C
507	G	A	A	A	A
528	A	T	A	A	A
534	C	A	T	T	T
543	T	C	C	C	T
546	T	A	A	A	A
552	A	A	C	A	A
594	T	C	C	C	C
630	C	T	T	T	T
640	C	T	T	T	T
653	T	T	T	C	C
771	T	C	C	C	C

Table 3. *Cont.*

Cyt b

Position	***E. akayima* sp. nov. (22)**	***E. murinus* (25)**	***E. beniensis* (7)**	***E. deschauenseei* (4)**	***E. notaeus* (8)**
783	C	A	C	C	CA
849	T	A	A	A	A
930	G	A	A	A	A
931	A	C	C	C	C
937	G	A	G	G	AG
969	T	C	T	T	T
1053	C	T	T	T	T

ND2

Position	*E. akayima* sp. nov. (28)	*E. murinus* (26)	*E. beniensis* (7)	*E. deschauenseei* (2)	*E. notaeus* (1)
31	C	T			
59	A	G	A	G	A
62	C	T	C	C	C
77	A	G	A	A	A
80	C	C	T	T	T
89	C	C	T	C	C
119	C	G	A	A	A
122	TA	T	A	C	C
131	G	A	A	A	A
143	T	T	C	C	C
158	C	T	C	C	C
159	T	C	C	C	
221	A	A	A	G	G
380	A	C	A	A	A
381	T	C	C	C	C
389	T	C	C	C	C
397	T	C	C	C	C
422	A	G	A	A	A
423	G	A	G	G	G
424	C	T	T	T	T
461	G	A	C	C	C
464	G	C	A	A	A
467	G	A	A	A	A
536	C	T	C	C	C
545	C	T	C	C	C
551	C	C	T	C	C
554	C	T	C	C	C
590	C	T	C	C	C
594	T	T	A	C	C
638	A	T	C	C	C
673	C	T	C	C	C
704	T	C	C	C	C
710	T	C	C	C	C
743	T	A	A	A	A
758	G	A	A	A	A
761	T	C	T	T	T
786	G	A	A	A	A
806	A	G	A	A	A
818	T	C	T	T	T
834	T	C	C	C	T
877	C	T	C	C	C
890	T	C	C	C	C

Table 3. *Cont.*

Cyt b					
Position	***E. akayima* sp. nov. (22)**	***E. murinus* (25)**	***E. beniensis* (7)**	***E. deschauenseei* (4)**	***E. notaeus* (8)**
947	G	A	C	C	C
961	T	C	C	C	C
968	T	C	C	C	C
991	T	C	C	C	C
ND4					
Position	*E. akayima* sp. nov. (22)	*E. murinus* (23)	*E. beniensis* (7)	*E. deschauenseei* (2)	*E. notaeus* (2)
44	C	T	C	C	
50	T	C	A	A	G
66	A	A	G	G	C
95	T	T	C	C	A
108	A	G	A	A	C
111	T	C	C	C	G
113	A	A	G	G	G
122	A	G	G	G	G
129	A	S	G	G	A
161	G	A	A	A	T
174	C	T	T	T	A
203	G	A	A	A	C
215	T	C	C	C	T
236	C	C	T	T	A
255	G	G	G	G	T
263	T	C	T	T	A
270	A	G	G	A	T
284	C	C	T	T	C
297	C	T	C	C	C
305	C	T	C	C	C
323	T	C	C	C	A
326	A	G	A	A	C
362	CT	A	C	C	
365	T	C	C	C	A
392	G	A	A	A	A
402	A	A	T	A	G
404	T	C	A	A	C
419	T	T	T	T	T
428	T	C	T	T	A
494	A	G	A	A	A
524	G	A	A	A	T
527	C	T	T	T	T
542	C	A	T	T	C
548	C	T	C	C	
593	T	C	C	C	C
605	C	T	C	C	A
626	T	C	A	A	C
680	C	T	C	C	T
692	C	T	T	T	A
750	G	A	A	A	A

Table 4. A morphological comparison of the holotype and paratype of *E. akayima* sp. nov. and the neotype of *E. murinus*.

	Eunectes akayima **sp. nov. (MCNG 1042) Holotype** [1]	***Eunectes akayima*** **sp. nov. (RMNH.RENA.20768) Paratype** [2]	***Eunectes akayima*** **sp. nov. (RMNH.RENA.29769) Paratype** [2]	***Eunectes murinus*** **(MPEG 27428) Neotype** [3]
Ventral	241	252	255	254
Subcaudal	53	45	69	66
Dorsal scales, anterior body	50	45	43	50
Dorsal scales, mid-body	60	61	56	58
Dorsal, posterior	41	38	40	42
Dorsal spots	94	96	116	94
Spots in contact	19	17	54	18
Supralabials	14/15	16/16	15/16	16/16
Infralabials	damaged	22 left side, right side is damaged	20/22	22/22
Infraoculars	damaged	2	1/1	2/2
In contact with eye	7/8	7	6/6	7/7
Suborbital	damaged	4	4/5	5/5
Supraocular	1/1	1	1/1	1/1

[1] Holotype is in UNELLEZ Museo de Ciencias Naturales, Venezuela. [2] Paratype is in Naturalis Biodiversity Center, Netherlands. [3] Proposed Neotype is in Museu Emilio Goeldi, Brazil.

3. Systematics

Article 13.1.1 of the ICZN requires that a description of the new species is given in the text of the paper, along with the diagnostic features that tell it apart from its sister taxa. Because the differences known at the time were all genetic, no morphological differences were identified as required by Article 13.1.1 in Rivas et al. [1]. Some authors consider that Article 13.1.1 has been met [11], while others consider that we did not, rendering *akayima* a nomen nudum [9]. We agree that we could have been more explicit on the diagnostic features identifying the new species and that the requirements of ICZN Article 13.1.1 were not met. Therefore, we validly describe the species in this note.

Class: Serpentes
Family: Boidae Gray, 1825
Genus: *Eunectes* Wagler, 1830

Remarks:

Dubois et al. [9] established that *Eunectes sensu* Wagler (1830) currently does not refer to anacondas, as the type species *Boa scytale* Linnaeus 1758, is not an anaconda They mention that they are planning to prepare a case for the International Commission of Zoological Nomenclature to fix Boa murina Linnaeus 1758 as its type species maintain the prevailing usage of *Eunectes* as a genus for anacondas. We follow Dubois et al. [9] and maintain the current use of *Eunectes* in this paper.

3.1. *Eunectes akayima* sp. nov.

Eunectes akayima nom. nud.—[1].
Eunectes aboma (Daudin, 1803)—[9], p. 36–37
Eunectes murinus (Linnaeus 1758)—[11]

Holotype: skin of a female, 485 cm in total length (TL), 428 in snout–vent length (SVL). MCNG 1042 (from UNELLEZ Museo de Ciencias Naturales, Venezuela), Venezuela, Apure State, Hato El Cedral, (7◦25′0.4″ N, 69◦19′51″ W), Leg. J. Rivas, 1993.

Paratypes: RMNH.RENA.20768 (Naturalis Biodiversity Center in the Netherlands), one male 283 cm in TL, 254.5 cm in SVL, with a stumpy tail. Specimen in alcohol, Suriname, Nickerie, Weg Amotopo, Karbalebo River Devis Val. Leg. M.S. Hoogmoed and JJP Paats 1980, MBUCV 7189. Female specimen in alcohol (Museo the Biología de la Universidad Central de Venezuela). Rio Cabrutica, Venezuela, Estado Guárico, Leg. A. Marcano 2006. RMNH.RENA.29769 (Naturalis Biodiversity Center in the Netherlands), one male, 204 cm in total length, 174 cm in SVL. Specimen in alcohol, Suriname, Zanderij, bij kreekje ("near a creek"). Leg H. Maas, date of collection: 4 March 1964.

3.2. Description

It is a large aquatic boid, with a relatively small head, dorsally located nostrils and eyes, and a dorsal color pattern that blends well with the aquatic vegetation. The head is differentiated from the body with a thinner neck, with small dorsal scales posteriorly and larger ones anteriorly (Figure 5), 14–19 supralabials separated from 2–3 infraoculars by a row of loreal (also called lorilabial) scales, 16–25 infralabials, 5–10 scales surrounding the eye, and 3–9 loreal scales. The prefrontals are longer than they are wide. There are 243–259 ventral scales, 61–78 subcaudals, 57–74 dorsal scales at the mid-body, and 80–148 dorsal blotches [1]. The coloration of the dorsal blotches may be lighter inside, even yellowish in the center as this trait is very variable within the species. The ventral coloration is light, yellowish in color with abundant black small spots. A streak about 1–2 scales wide extends from the eye towards the jaw, and above it, there is a wider stripe often red or orange but can be lighter, including olive green.

Figure 5. The head of the *E. akayima* sp. nov. paratype (RMNH.RENA.20768) at the Naturalis Biodiversity Center.

3.3. Dimensions

It exhibits a strong sexual size dimorphism. Males never exceed 3.5 m in length. Females are much larger, often exceeding 4 m, and can reach lengths in excess of 6 m (Table 1) [12,22]. Relative tail length (tail/snout–vent length) in adult females was 0.1388 (SD 0.0107) and 0.1731 (SD 0.0127) in males (Table 2).

3.4. Morphological Cross-Diagnosis

Rivas et al. [1] mention that there are no reliable morphological diagnostic traits to differentiate *E. akayima* sp. nov. and *E. murinus,* which is the only close relative. However, further investigation revealed several morphological differences between the species. *Eu-*

nectes murinus males may grow to a larger size, in excess of 3.5 m, while *E. akayima* sp. nov. males never reach that size (Figure 6). Thus, large males can be differentiated based on total length. Males of *E. akayima* sp. nov. are on average 253.5 cm (N = 353), which is significantly smaller than the average length of *E. murinus* males (279.0, Table 1, n = 66). In addition, the coefficient of variation (CV) may be calculated to compare the variance of a variable across distinct means [24]. The CV of male *E. akayima* sp. nov. (0.126) is significantly smaller than that of males *E. murinus* (0.224, t = 15.7, df 380, $p < 0.0000$), demonstrating substantial differences in the size variance they exhibit (Table 1). Figure 6 shows the SSD of both species where we can see that the overlap in sizes among males and females is far larger in *E. murinus* than in *E. akayima* sp. nov. Furthermore, the tail length of *E. akayima* sp. nov. is longer than that of *E. murinus* (Ancova with SVL as a covariate, F = 20.347, df: 232, $p < 0.0000$, Table 5), and the allometric growth of the tail differs significantly between females of *E. akayima* sp. nov. and *E. murinus* (Table 6). The relative length of the tail (tail length/snout–vent length) decreases in both species as they grow larger, but this decrease is steeper in female *E. murinus* (Figure 7) and can be confirmed in the significantly different values of the slopes and intercept of their regressions (Table 6).

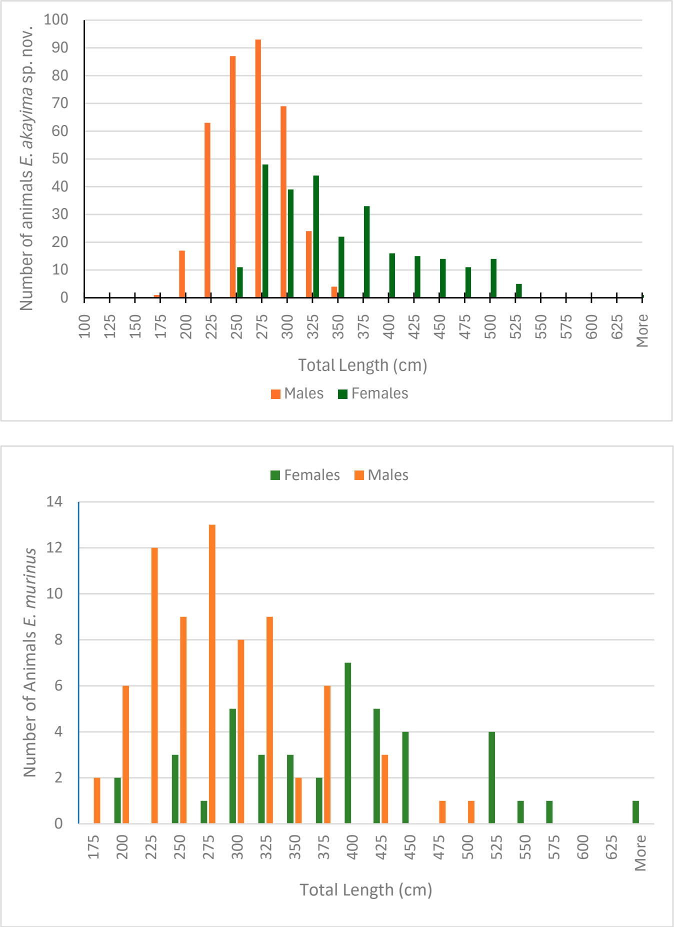

Figure 6. A comparison of SSD between both species of green anaconda. Notice that only a few females are longer than the longest males in *E. murinus* while in *E. akayima* sp. nov. most females are longer than the longest males. In addition, the variance of size in males in *E. murinus* is substantially larger than that of *E. akayima* sp. nov. Data from *E. akayima* sp. nov. are from [16], and data from *E. murinus* are from unpublished data from JT and LP as PC. This histogram includes data from museum specimens used in Pizzatto-do-Prado [19] as well as from animals measured live. Because extracting the skin often involves stretching, the length of the largest specimens was estimated from head size regressions to avoid the bias of skin stretching during preparation.

Table 5. A comparison of tail length (cm) between adult *E. murinus* and *E. akayima* sp. nov. SD = standard deviation, N = sample size, Min = minimum value, Max = maximum value. CV is the coefficient of variation that is calculated by dividing the standard deviation by the mean, LCI the lower 95% confidence interval, and UCI the upper 95% confidence interval. Data from *E. akayima* sp. nov. are from [16], and data from *E. murinus* are from [13,14,19]. For this table, we combined data from live and preserved specimens.

	Mean	**SD**	**N**	**Min**	**Max**	**CV**	**LCI**	**UCI**
E. akayima sp. nov. female	43.39	8.17	78.00	26.51	64.00	0.1883	41.58	45.21
E. murinus female	37.69	3.85	24.00	27.10	44.00	0.1021	36.07	39.32
E. akayima sp. nov. male	37.34	4.43	104.00	26.97	46.00	0.1187	36.49	38.19
E. murinus male	37.57	3.25	21.00	23.20	61.00	0.0865	36.09	39.05

Table 6. Regression comparisons of relative tail length (tail length/snout–vent length) for *E. akayima* sp. nov. and *E. murinus*. Data from *E. akayima* sp. nov. are from [16], and data from *E. murinus* are from [13,14].

		Coefficients	**Standard Error**	**t Stat**	***p*-Value**	**Lower 95%**	**Upper 95%**
E. akayima sp. nov. female	Intercept	0.1677	0.0046	36.8097	0.0000	0.1586	0.1767
	Slope	−0.0001	0.0000	−6.4963	0.0000	−0.0001	−0.0001
E. murinus female	Intercept	0.2562	0.0294	8.7251	0.0000	0.1953	0.3171
	Slope	−0.0035	0.0008	−4.4881	0.0002	−0.0052	−0.0019
E akayima sp. nov. males	Intercept	0.2177	0.0084	25.9943	0.0000	0.2011	0.2343
	Slope	−0.0002	0.0000	−5.3768	0.0000	−0.0003	−0.0001
E. murinus males	Intercept	0.2079	0.0132	15.7595	0.0000	0.1807	0.2351
	Slope	−0.0002	0.0001	−4.3263	0.0002	−0.0004	−0.0001

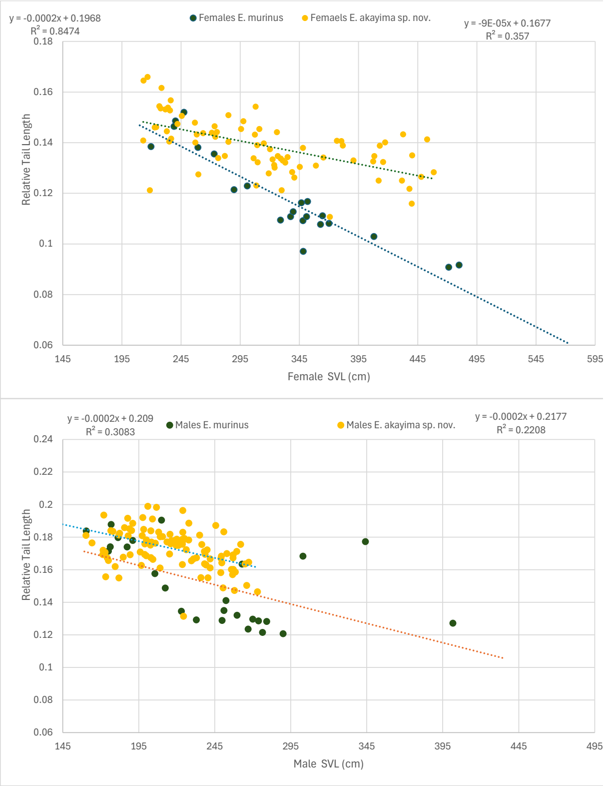

Figure 7. Relative tail length of *E. akayima* sp. nov. and *E. murinus* showing differences in allometric growth. Data on *E. akayima* sp nov. are from [16], and data from *E. murinus* are from [13,14].

3.5. Molecular Cross-Diagnosis

Eunectes akayima sp. nov. can be distinguished from *E. murinus* by molecular characters. Cytochrome b (Cytb) sequences yielded 37 molecular diagnostic characters between position 1 and 1053 (Table 3) with a pairwise sequence divergence with *E. murinus* of 5.24% (Table S2 in [1]). NADH 2 (ND2) sequences yield 40 molecular diagnostic characters between position and 991 with a pairwise sequence divergence with *E. murinus* of 5.27% (Table 3). NADH 4 (ND4) sequences yielded 32 molecular diagnostic characters between position 1 and 750, with a pairwise sequence divergence with *E. murinus* of 5.19%. Over the three mitochondrial genes (2923 bp in total), there are 109 nucleotide differences that distinguish *E. akayima* sp. nov. from *E. murinus*, with an overall pairwise genetic divergence of 5.5%.

Molecular diagnostic characters used to distinguish *E. akayima* sp. nov. from *E. murinus* include the following autapomorphies for *E. akayima* sp. nov.: G, T, T, T, C, T, G, C, T, and T in Cytb at corresponding nucleotide positions of 258, 273, 305, 307, 339, 444, 507, 534, and 594, while *E. murinus* has A, C, C, C, T, C, A, A, and C in the same positions (Table 3). Additionally, the new species is further distinguished by autapomorphies in ND2: C, G, G, G, A, T, and T at corresponding nucleotide positions of 424, 461, 464, 467, 638, 704, and 710 versus T, A, C, A, T, C, and C in *E. murinus* (Table 3). The position numbers refer to aligned sequence gene sets (GenBank accession #s in Table S1 of Rivas et al. [1]). A summary of all molecular diagnostic characters for *E. akayima* sp. nov. and *E. murinus* is detailed in Table 3, along with autapomorphies characterizing *E. murinus* and additional diagnostic characters distinguishing between green and yellow anaconda species *sensu* Rivas et al. [1].

3.6. Etymology

The word for anaconda in various Cariban languages is a variant of *akayima*/*okoyimo*/*okoimo*, in which a*kayi*/*okoyi*/*okoi* means "snake" and the suffix -*ima*/-*imo* means "large or great". The literal translation of *akayima* is "The Great Snake" [1]. The species name *akayima* is pronounced as follows: əkəyimə in standard dictionary pronunciation font; ŭkŭyēmŭ using the phonics; and uh-kuh-yee-muh using the Plotkin method for English-like writing to capture Cariban language pronunciations [36]. The word akayima is also used to refer to the rainbow, probably associated with a feathered serpent in their belief system that came out after rains to dry its feathers [37]. We, therefore, acknowledge the culture of these Indigenous people who share their territories with this species by adopting their word for anaconda as the specific epithet for this new species, which is a noun in apposition.

3.7. Distribution

The distribution included Ecuador (Amazon Basin), Venezuela, Guyana, Suriname, French Guiana, and Trinidad (all Orinoco Watershed).

3.8. Remarks

Some of the morphological characters used to distinguish the new species from *E. murinus* can only be used to distinguish them at the population level. To identify individual snakes, relative tail length, the maximum size of the males, and genetic differences can be used.

4. Discussion

In this contribution, we aimed to provide the information missing in Rivas et al. [1] and to validly describe *E. akayima* sp. nov. in compliance with the ICZN [10]. We also designated a neotype for *E. murinus* to stabilize the group and provided morphological differences between both species. We hope that our contribution will help fix the taxonomy of anacondas and shed light on the nature of these two species.

In our original paper, we claimed that there were no morphological or diagnostic differences between these two species that could be reliably used to identify the two species. However, while carrying out the present study, we have come to realize that morphological differences indeed exist in the form of size, SSD, and allometric growth.

These morphological differences put to rest any doubt that there are two different species. While SSD may show plasticity [38], it is highly conserved in boas [18,19]. Moreover, our data on *E. murinus* is limited compared with *E. akayima* sp. nov., and increasing the sample size will only make the standard error smaller and strengthen the differences found. Some of the males of *E. murinus* (Figure 1) are about 50% larger than the largest males of *E. akayima* sp. nov. Considering that even with a limited sampling of *E. murinus* the detection of a meaningful trend of longer males is possible, it is strong evidence that the trend is legitimate. In addition, allometric growth differences are not known to be plastic. Taken together, these differences confirm the distinctiveness between both species.

De Queiroz [39] elaborated on how all species concepts are about two lineages somehow reproductively isolated while stressing the importance of such isolation in defining new species. While better sampling of contact zones and genomic data would be desirable, the difference between *E. akayima* sp. nov. and *E. murinus* is supported by not only the substantial mDNA divergence, separation time, and morphology but also by a consistent biogeographic scenario separating these two lineages, as well as many others. The rising of the Vaupés arch (10–8 mya), connecting the Andes with the Guyana shield just south of the current course of the Guaviare River, produced what is known as the Orinoco–Amazon vicariant event [40,41]. This vicariant event is responsible for the separation of numerous aquatic taxa into different species following the same biogeographic pattern including Prochilodontidae fishes (Characiforme) [40,41], Cyprinodontoidei fishes (Cyprindodontiforme), [42], catfishes [43], Serrasalmidae fishes (Characiforme) [44], turtles [45], gecko lizards [46], and Anole lizards [47], as well as arboreal snakes [48] in addition to other taxa cited in Rivas et al. [1].

While the Vaupés arch is still dividing both watersheds, its relief is hardly noticeable due to sedimentation by alluvial mega fans from the Guaviare River in the north and the Guayabero and Caquetá rivers in the south [49]. Currently, both watersheds connect via the Casiquiare River which flows from the Orinoco into the Rio Negro, which subsequently flows into the Amazon [50]; this is likely how *E. akayima* sp. nov. dispersed to Ecuador. However, this sedimentation of the slopes of the Vaupés arch is rather recent. At first, most sediments came from the Proterozoic and highly eroded Guyana shield which provided very little sediments [49,51]. It was only when the Andes became a mountain ridge high enough to produce orogenic precipitation that the Andean sediments started to come in abundance into the basin. This did not start until the Pliocene (approx. 6–5 mya) [52,53]; therefore, the vicariant event lasted several million years. This is substantially different from vicariant events associated with glaciation, which are common in the northern hemisphere. First, because the Pleistocene, and its glaciation, lasted only 2.6 my, the duration of the actual vicariant events (the glaciation) was only in the thousands of years. These shorter separation times may or may not produce genetic isolation and irreversible separation needed for the two lineages to be considered different species; thus, there would be a need to carefully study the contact zone and possible interbreeding. The Orinoco–Amazon vicariant event lasted more than enough time to produce the irrevocable separation needed to split two species, which indeed it did across a wide variety of taxa, as cited above. There is no reason to think that green anacondas would be an exception to this region-wide pattern of speciation that affected many other aquatic taxa all over the northern part of the continent.

What Is in a Name

We have demonstrated that *E. akayima* sp. nov. is a valid species and shown that other synonyms that have been used for anacondas either do not refer to this species or are impossible to identify (*nomina dubia*). Our original stance of choosing the Indigenous name 'akayima' and treating it as the senior synonym, while controversial, signified an attempt to move towards rectifying long-standing biases within the scientific domain. We did not accept the notion that a name given by a person that only knew the snake from a jar and never saw it alive would take precedence over the name given by those who lived with the snake and interacted with it on a regular basis. This begs the question: is it enough to know nomenclature to classify an organism without having much knowledge of the organism itself?

In the current state of affairs, it seems that giving parity to Indigenous names over those given by Western scientists is viewed as suspect and controversial. We are surprised that the critical opinion article by Dubois et al. [9] was published less than a month after ours. This paper of 51 pages was submitted to the Journal Bionomina on March 4 2024 by Alain Dubois, the founder and chief editor of the Bionomina s, along with six other authors, three of which are editorial board members of the same journal. It was accepted on March 8, 2024. It would certainly seem impossible to obtain 2–3 independent reviews in that short period. Combined, the short review process and presence of the editor as the lead author of a paper, raises legitimate ethical concerns and does seem to compromise the integrity of the journal. This is surprising because the paper would probably have been accepted in a reputable journal following independent peer review, though it would not have been published as quickly. Since Dubois et al. [9] went beyond highlighting, discussing, and fixing the errors in our initial paper, we are under the impression that concerns about the name *E. akayima* sp. nov. may have contributed to their haste. Dubois et al. [9] neatly document how early taxonomists who did not know much about the species they were describing created confusion. This is true even with Linnaeus, the creator of the binomial system of nomenclature. This illustrates that expertly knowing nomenclature procedures cannot substitute for adequate knowledge of the species they are classifying. Case in point, due to their lack of knowledge of anacondas, Dubois et al. [9] confused *B. aboma* (*E. murinus*) with *E. akayima* sp. nov., thus creating additional confusion despite their intimate knowledge of ICZN. Unfortunately, we fear that those offended by the use of an Indigenous name for *E. akayima* sp. nov. will continue to attempt to change it under the excuse of “avoiding taxonomic instability” which ironically will foster the taxonomic instability they claim to want to avoid.

5. Conclusions

We continue to hold that we have effectively demonstrated the existence of a second species of green anaconda. In addition, we have found evidence of morphological differences which supports the distinctiveness of both species. While our first attempt to describe the species was not in full compliance with the ICZN, we have now demonstrated that *E. akayima* sp. nov. is a valid name and validly described it under the ICZN. In addition, we have corrected some errors we made as well as providing additional evidence to support our initial claims. We also provided a neotype for *E. murinus* to bring stability to the group. We realize that all scientific claims are open to revision or rejection as new knowledge becomes available, though we feel that this must be based on solid scientific evidence and not just authoritative pronouncements without data support. We hope that all this information can be used by taxonomists, biologists, and conservationists alike to continue studying and protecting these fascinating species. The occurrence of *Eunectes akayima* sp. nov. could also be used as an argument to reconsider protection and management guidelines for the northern section of the Amazonia/Orinoquia system.

This paper has been registered in ZooBank to meet the requirements of electronic publication by the International ICZN of Zoological Nomenclature. The publication LSID is: urn:lsid:zoobank.org:pub:F47FAF30-3601-47A7-B9EC-0D9359D23DBB. The nomenclatural act LSID for the species description is urn:lsid:zoobank.org:act:004D5E05-D3D5-4685-BC7D-E82088E31FCD.

Author Contributions: Conceptualization, J.A.R. and S.C.-R.; methodology J.A.R. and J.S.T.; validation, J.A.R., P.S.C. and F.J.V.; formal analysis, S.C.-R., M.R. and J.A.R.; investigation, J.A.R., M.R. and S.C.-R.; resources, R.L.-P., F.J.V., L.F.P., P.D.L.Q. and P.C; data curation, S.C.-R. and J.A.R.; writing—original draft preparation, J.A.R. and M.R.; writing—review and editing, J.A.R., P.D.L.Q., M.M., P.S.C., J.S.T., G.M.B., F.J.V., R.L.-P., J.E.G.-P., B.G.F. and S.C.-R.; visualization, J.A.R., S.C.-R., M.M. and J.S.T.; supervision, J.A.R. and B.G.F.; funding acquisition, J.A.R., S.C.-R. and B.G.F. All authors have read and agreed to the published version of the manuscript.

Funding: Sampling conducted by PSC in the Madre de Dios region of Peru was supported by MITACS international in collaboration with the Amazon Rainforest Conservancy and the Environmental Systems Research Institute (Esri).

Institutional Review Board Statement: Animal handling was carried out and tissues were obtained under IACUC protocol at the New Mexico Highlands University, Approval 2012/7-12-2012, and the University of Queensland, Animal Ethics Approval 15/03/2021/AE000075. Registration of *E. akayima* sp. nov. in ZooBank: A58A262E-2E07-48D3-B712-209CCDFFD038. Permit for working on Indigenous land in Ecuador: MAATE-DBI-CM-2022-0259.

Data Availability Statement: All data used in this study has been uploaded as supplemental material. All GenBank accession numbers of gene sequences used in previous work are available in the Supplementary Materials of Rivas et al. [1].

Acknowledgments: We thank Ligia Pizzato do Prado for generously sharing unpublished data. We thank Kathy Gray for archival assistance. We also thank all the taxonomists who provided help and guidance but asked not to be mentioned for fear of retaliation and bullying. We thank Juca Ygarapé for assistance in the field and access to the Bonito study site and everyone who helped during the samplings in the area. We appreciate the assistance and support provided by staff members and concession stewards at the Los Amigos Biology Station and on the Las Piedras River at the Las Piedras Amazon Centre. In particular, we appreciate the logistical support provided by the Alliance for Research and Conservation in the Amazon and Junglekeepers Peru S.A.C.

Conflicts of Interest: The authors declare no conflicts of interest.

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