Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Zoologia

Evolution of Caudal Luring in Viperidae OPPEL 1811

Aída Pereira Giozza

Orientador: Reuber Albuquerque Brandão

Brasília – DF

Setembro de 2020

Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Zoologia

Evolution of Caudal Luring in Viperidae OPPEL 1811

Aída Pereira Giozza

Orientador: Reuber Albuquerque Brandão

Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Zoologia da Universidade de Brasília, como requisito para a obtenção do título de Mestre em Zoologia.

Brasília – DF

Setembro de 2020

Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Zoologia

Dissertação de Mestrado

AÍDA PEREIRA GIOZZA

Título:

Evolution of Caudal Luring in Viperidae OPPEL 1811

Banca Examinadora:

Prof. Dr. Reuber Albuquerque Brandão
Presidente/ Orientador
ZOO/UnB

Dr. Laura Rodrigues Vieira de Alencar
Membro Titular
Department of Biological Sciences/Clemson University

Prof. Dr. Julia Klaczko
Membro Titular
CFS/UnB

Prof. Dr. Angele dos Reis Martins
Membro Suplente
CFS/UnB

Aos meus pais, que sempre me guiaram pelo caminho da educação, e fizeram com que essa trajetória fosse um pouco mais fácil. Dedico, ainda, aos meus avós Antônio Pereira, Zeni Pereira, Wilson Giozza (já falecidos) e Elma Giozza.

AGRADECIMENTOS

Agradeço, primeiramente, à minha família, especialmente aos meus pais, William e Silvana, por terem me possibilitado chegar onde cheguei. Vocês são minha grande inspiração. Ao meu irmão Thomas, pela parceria e companheirismo mesmo à distância, e por ter me dado uma casa para fugir quando eu precisava espairecer (ou um teto para cuidar de 100 rãs antes do transporte). Amo vocês.

Ao meu orientador, Reuber Albuquerque Brandão. Por ter me aceitado quando eu ainda era uma jovem recém-graduada sem saber muito para onde ir. Por ter me dito que é no mestrado que se ganha experiência (dito e feito!). Muito obrigada pela orientação e compreensão nesses últimos dois anos. Espero poder manter a parceria nos anos que virão.

À minha orientadora de consideração, Veronica Slobodian. Eu caí de paraquedas nesse mundo de filogenias, R e métodos comparativos. Muito obrigada por me resgatar, e por responder pacientemente todas os meus (muitos) questionamentos, e me guiar por um mundo inteiramente novo e cheio de possibilidades. Com você aprendi que "vermelho é amor" (apesar de eu preferir azul e preto hahaha) e que o relacionamento com o R é sempre complicado, mas que tudo se ajeita. Foi um prazer conhecê-la. Que essa nossa parceria possa se repetir várias vezes.

À minha madrinha, Germana Henriques Pereira, por todo o carinho, pelo apoio de sempre e por me receber em sua casa sempre que eu precisei. Ao Rafael Timóteo de Sousa Júnior por ter me apoiado e se feito presente, tanto como meu padrinho, quanto como coordenador do laboratório LATITUDE, auxiliando como pôde. À Marina, minha prima querida, pelos momentos de descontração proporcionados. Um beijo especial pro Cacá! Também amo vocês.

Ao Carlos Eduardo Nóbrega (Cadu), não só pela tutoria dos animais coletados neste mestrado quando o projeto ainda era outro, mas também pelos ensinamentos e pela parceria! Espero poder continuá-la e fazê-la crescer futuramente.

Muito obrigada a todos que me auxiliaram de uma maneira ou de outra com as minhas questões e dúvidas decorrentes do mestrado, incluindo a identificação de algumas espécies. Em especial ao Wellington, que me ajudou pacientemente diversas vezes, inclusive durante a madrugada, e à Lílian que acabou virando alvo das minhas perguntas desesperadas sobre metodologia. Lílian, muito obrigada por tudo, perdoe as bagunças na sua casa e as viagens de última hora. Sou muito feliz por ter te conhecido, cuida bem aí do Mew, da Nix e de Thomas!

Aos professores do Departamento de Zoologia pelos momentos de confraternização, cafés e conselhos, em especial ao Prof. José Roberto Pujol Luz, por ter me abrigado em seu laboratório em diversas ocasiões e pelas conversas e zoeiras de futebol – dá-lhe Grêmio (e Liverpool)!

Á Jade Cristine (Jaja), pela amizade, companheirismo e todo auxílio que me deu nos últimos anos. Por ter aceitado ser minha estagiária, além de melhor amiga durante todo esta trajetória do mestrado. Por embarcar em todas as minhas loucuras de prontidão, por ser aquela que "Bora? Bora!". Por ter segurado a barra na hora do choro, da raiva e da impaciência. Por ter estado presente também na maior parte das horas boas, treinos, rolês, bebedeiras, campos, etc. Obrigada por fazer tudo ser mais fácil e mais engraçado.

A Mickaella Martins (Mimi) e Ingrid Pinheiro, que, mesmo estando longe, deram um jeito de se manter presentes em minha vida, inclusive quando eu mais precisava. Gosto muito muito muito de vocês!

Ao Alexandre Ariel, por me acompanhar desde o início da minha graduação. Por todos os conselhos (por minha conta e risco, claro!), saídas e caronas. Por ter sido uma constante neste mar de incertezas que tive ao longo dos anos. Pela sua inestimável amizade. E por compreender todos os perrengues que passei nesse mestrado, tendo vivido parte deles.

Aos meus amigos que, apesar do distanciamento, eu sempre mantive o apreço: Danielly Teles, Luisa Miranda, Carol Hildebrand, Mille Montenegro, Luis Renato "Jesus", Marcelo Moussallem, Pedro "Paraca", Glabis Pereira, Bernardo "Tristinho", Rogério Yamassaki e Fábio Vianna.

Ao pessoal do LAFUC, pelo companheirismo e por terem feito a convivência no laboratório ter sido, principalmente, divertida e descontraída. Em especial aos colegas e amigos Nathalie Citeli, Andrei Guedes, Afonso Santiago, Júlia Batalini, Ana Cecília Holler, Mateus Alencar e Gabriela Carvalho. Precisamos fazer aquele campão de imersão na Chapada! Also, thanks to Maud Demarest for the help she gave me during this work, it was very nice to meet you! I hope we can get together sometime in the future.

À galera do campão, por terem se disponibilizado a me ajudarem com todos os trabalhos de campo, mesmo que fosse a noite, com chuva ou um frio gelado. Existe um grau de aproximação que só se atinge quando você afunda na lama com alguém. Vocês fizeram com que o trabalho fosse divertido, e facilitaram muito a minha vida acadêmica e pessoal.

Ao Joshua, por ter sido um grande presente que a biologia deu para mim. Por ter segurado minha mão e me feito continuar todas as vezes que pensei em desistir. Por ouvir todas as minhas reclamações (com ou sem paciência haha), choros e esperneios, e sempre dizer que eu iria conseguir. Por botar minha cabeça no lugar quando eu precisei. Por me acompanhar nas minhas vitórias e me amparar nas minhas derrotas. Por ter sido, sempre, meu torcedor de carteirinha. Por dizer que vai ficar tudo bem. Por acreditar mais em mim do que eu mesma. Por ter aparecido. E por ter voltado. Amo você.

Por fim, agradeço às instituições de fomento Coordenação de Aperfeiçoamento de Pessoal e Nível Superior (CAPES) pela bolsa de mestrado concedida, à Fundação de

Apoio à Pesquisa do Distrito Federal (FAPDF) pelo apoio financeiro fornecido para participar do Congresso Mundial de Herpetologia, ao Decanato de Pós-Graduação da Universidade de Brasília e à Pós-Graduação em Zoologia (UnB), pelos apoios financeiros que possibilitaram o desenvolvimento dessa pesquisa. Agradeço também ao Laboratório LATITUDE do Departamento de Engenharia Elétrica pelo empréstimo do computador no qual as análises foram rodadas pois, sem ele, eu não teria conseguido concluir este trabalho. Agradeço, ainda, à Fundação Jardim Zoológico de Brasília pelo cuidado com os animais coletados durante o meu Mestrado, em especial aos tratadores do Serpentário. Agradeço também a secretaria e coordenação da Pós- Graduação em Zoologia pelos serviços e auxílios prestados, e aos servidores da Faculdade de Tecnologia por sempre manterem limpo e organizado o Laboratório de Fauna e Unidades de Conservação.

“Don’t let the muggles get you down.”

- *Ron Weasley*

“Just keep swimming.”

- *Dory*

“Mas a dúvida é o preço da pureza
E é inútil ter certeza”

- *Humberto Gessinger*

“I used to think anyone doing anything weird was weird. Now I know that it is the people that call others weird that are weird.”

- *Paul McCartney*

LISTA DE TABELAS

LISTA DE FIGURAS

ausentes. Colorido: caracteres presentes. Gráficos nos nós representando as probabilidades posteriores de cada estado.

Figura 10. Árvores espelhadas com a reconstrução do estado ancestral de cauda conspícua (CC, esquerda) e mudança ontogenética na dieta (MOD, direita), de acordo com o modelo ARD de taxa de transição entre estados de caracteres. Preto: caracteres ausentes. Colorido: caracteres presentes. Gráficos nos nós representando as probabilidades posteriores de cada estado.

Figura 11. Detalhe da ponta da cauda de *Pseudocerastes urarachnoides* que se assemelha a um aracnídeo.

Figura 12. Exemplos de caudas conspícuas (CC), mas que não mimetizam itens alimentares de presas das serpentes. A: *Crotalus ruber*, B: *Crotalus atro,* C: *Trimeresurus insularis* e D: *Crotalus horridus.*

Figura 13. Espécies que apresentam engodo caudal (EC) mas não possuem mudança ontogenética na dieta (MOD). A: *Bitis caudalis*, B: *Cerastes vipera*, C: *Bitis peringueyi* e D: *Bitis schneideri*.

Figura S1. Árvore filogenética para engodo caudal (EC) ilustrando os números dos nós cujos valores de probabilidade posterior de cada estado estão referenciados na tabela S1.

Figura S2. Árvore filogenética para cauda conspícua (CC) ilustrando os números dos nós cujos valores de probabilidade posterior de cada estado estão referenciados na tabela S2.

Figura S3. Árvore filogenética para mudança ontogenética na dieta (MOD) ilustrando os números dos nós cujos valores de probabilidade posterior de cada estado estão referenciados na tabela S3.

RESUMO

Título: Evolução do Engodo Caudal em Viperidae OPPEL 1811
Autor: Aída Pereira Giozza
Orientador: Reuber Albuquerque Brandão, Dr.
Programa de Pós-Graduação em Zoologia
Brasília, 24 de setembro de 2020

Serpentes apresentam diversas estratégias de forrageamento, podendo ser forrageadoras ativas ou do tipo senta-e-espera. O mimetismo agressivo é uma estratégia de forrageamento por emboscada que está presente em diversos taxa. Um tipo de mimetismo agressivo ocorre quando o predador imita itens alimentares de sua presa para atraí-la. O engodo caudal (EC) é a forma mais comum de mimetismo agressivo dentre as serpentes, especialmente na família Viperidae. O EC consiste na atração de presas que se alimentam de animais semelhantes a vermes, por uma serpente de coloração críptica, que realiza movimentos ondulatórios com a sua cauda de coloração conspícua. Ocorre, geralmente, em serpentes juvenis que também apresentam mudanças ontogenéticas na dieta (MOD), de presas ectotérmicas para presas endotérmicas. Vários autores supuseram que a presença de EC está correlacionada a caudas conspícuas (CC) e MOD, mas tal correlação nunca foi testada. Neste trabalho, eu investiguei os padrões de origem e persistência de EC, CC e MOD ao longo da evolução de Viperidae, medi o sinal filogenético e testei se, de fato, há correlação entre tais caracteres. Para tal, busquei na literatura cientifica pela presença ou ausência de EC, CC e MOD para 263 espécies de viperídeos e organizei tais informações em uma matriz de dados. Também utilizei sites de ciência cidadã e divulgação científica com identificação confiável de espécies. Usei métodos filogenéticos comparativos para medir o sinal filogenético dos três caracteres, para testar se há correlação entre cada par de caracteres, assim como para reconstruir os estados de caracteres ancestrais para a família Viperidae por meio de parcimônia e máxima verossimilhança. Encontrei que todos os caracteres têm sinal filogenético forte, mostrando que a evolução de tais caracteres está mais correlacionada às relações filogenéticas dentro de Viperidae do que a restrições ecológicas atuais. Além disso, encontrei correlação significativa entre todos os pares de caracteres, corroborando sugestões de trabalhos anteriores. A reconstrução por máxima verossimilhança indicou que o ancestral de Viperidae possuía todos os três caracteres estudados, enquanto a reconstrução feita por parcimônia retornou o ancestral da família com EC e CC, mas sem MOD. Estudos que tragam mais informação sobre a história natural de serpentes contribuirão para o entendimento da evolução de Viperidae.

Palavras-chave: Reconstrução de caracteres ancestrais, mudanças ontogenéticas na dieta, cauda conspícua, métodos filogenéticos comparativos, mimetismo agressivo.

ABSTRACT

Title: Evolution of Caudal Luring in Viperidae OPPEL 1811
Author: Aída Pereira Giozza
Supervisor: Reuber Albuquerqur Brandão, Dr.
Post-Graduate Program in Zoology
Brasília, September 24, 2020

Snakes present numerous feeding strategies. They can be active or sit-and-wait foragers. Aggressive mimicry is an ambush strategy that is present in various animal taxa. There are several examples of aggressive mimicry throughout the animal kingdom, one of which happens when the predator mimics food items of an eventual prey to attract it. Caudal luring is the most common form of aggressive mimicry among snakes, especially in the Viperidae family. Caudal luring is the attraction of prey that feeds on worm-like invertebrates by a cryptically colored snake that waves a conspicuous tail tip. It is often performed by juvenile snakes that also present ontogenetic shifts in diet from ectothermic to endothermic prey. Several authors assumed that the presence of caudal luring (CL) is correlated to conspicuous tail tips (CTT) and ontogenetic shifts in the diet (OSD), but that correlation was never tested. Herein, I investigated the pattern of origin and persistence of CL, CTT, and OSD along Viperidae evolution, measuring their phylogenetic signal as well as testing if there is indeed a correlation between these characters. I searched for information about the presence or absence of CL, CTT, and OSD in the scientific literature for 263 species of viperids found in Alencar *et al.* (2016) phylogeny, and assembled it in a data matrix. I also used websites of citizen science and scientific popularization that had reliable species identification. I used Phylogenetic comparative methods to measure the phylogenetic signal of the three characters, to test if there is a correlation between each pair of characters, as well as to reconstruct the ancestral character state for the family Viperidae using parsimony and maximum likelihood. I found that all characters have a strong phylogenetic signal, which means that the evolution of the characters is more correlated to the shared evolution inside Viperidae than to ecological constraints. Also, I found there is significant correlation between all the pairs of characters, which corroborates suggestions made previously in the literature. Maximum likelihood reconstruction returned that the ancestor of Viperidae presented all three characters, while the parsimony approach indicated the viperid ancestor having CL and CTT but without OSD. Studies that bring further information on the natural history of viperid snakes should contribute to enrich and complement the knowledge on Viperid evolution.

Keywords: Ancestral character reconstruction, ontogenetic shifts in diet, conspicuous tail tips, phylogenetic comparative methods, aggressive mimicry.

INTRODUÇÃO GERAL

Mimetismo agressivo como estratégia de forrageamento

Predadores ao longo de todo o reino animal apresentam variadas estratégias para captura e subjugação de suas presas (Glaudas & Alexander, 2016). O mimetismo agressivo é uma estratégia de forrageamento utilizada por alguns predadores (Greene, 1997), que ocorre quando o predador evita ser detectado por suas presas por causa de sua semelhança com a própria presa, ou com algo que é neutro ou benéfico para a presa em questão (Ramya, Kumar, Keerthi, Srinivasa & Ramesh, 2017). Este tipo de estratégia se estabelece porque, quando a presa é enganada pelos sinais emitidos pelo predador, o predador é beneficiado (Glaudas & Alexander, 2016).

Existem vários exemplos de mimetismo agressivo no reino animal. Dentre as aves, indivíduos da espécie *Lanius excubitor* LINNAEUS, 1758 atraem passeriformes de menor tamanho para servirem de presa ao imitar sua vocalização durante o inverno, uma forma de mimetismo agressivo que também pode ser chamada de “atração acústica” (Atkinson, 1997). Outro exemplo de “atração acústica” acontece no ortóptero *Chlorobalius leucoviridis* TEPPER, 1896, que imita os sinais acústicos feitos por cigarras da tribo Cicadettini para atrair machos de cigarra que estão à busca de fêmeas receptivas (Marshall & Hill, 2009). Hemípteros da espécie *Stenolemus bituberus* STÅL, 1874 criam vibrações em teias de aranha para atraí-las e predá-las (Wignall & Taylor, 2011). Bioluminescência é também usada como isca por diversos animais aquáticos, incluindo alguns peixes, lulas e polvos (Haddock, Moline & Case, 2010).

Uma interessante forma de mimetismo agressivo ocorre quando o predador atrai sua presa simulando itens alimentares comuns a estas presas (Ramya *et al.* 2017). Tartarugas-aligátor (*Macrochelys temminckii*) usam um apêndice da língua com forma semelhante a uma larva para atrair peixes (Harrel & Stringer, 1997). Algumas aranhas usam suas teias para imitar o padrão e/ou as cores dos alimentos de suas presas(Jackson, 1992; Ramya *et al.* 2017).

As serpentes são animais exclusivamente carnívoros (Marques, Eterovic & Sazima, 2019) e apresentam diversas estratégias de forrageamento. Serpentes podem ser forrageadoras ativas, o que significa que se movimentam no ambiente em busca de presas, capturandoas quando encontradas (Lillywhite, 2014). Serpentes também podem ser forrageadoras do tipo "senta-e-espera", buscando locais com maior concentração de presas, onde possam aguardar a oportunidade de alimentação, emboscando presas (Lillywhite, 2014). Algumas espécies de serpentes "senta-e-espera" empregam mimetismo agressivo, como por exemplo aquelas que realizam engodo lingual (atração de presas via movimentos da língua), incluindo *Nerodia clarkii* (BAIRD & GIRARD, 1853), *Nerodia rhombifer* (HALLOWELL, 1852), *Nerodia sipedon* (LINNAEUS, 1758), *Thamnophis atratus* KENNICOTT, 1860, *Thamnodynastes strigatus* (GÜNTHER, 1858) e *Bitis arietans* MERREM, 1820 (Mario-da-Rosa *et al.* 2020).

Dentre as serpentes, engodo caudal é a forma mais comum de mimetismo agressivo, o qual consiste na atração de presas que se alimentam de animais semelhantes a vermes, por uma serpente de coloração críptica, que realiza movimentos ondulatórios com sua cauda de coloração conspícua (Heatwole & Davison, 1976; Reiserer & Schuett, 2008). Se bem sucedida, a presa irá confundir a ponta da cauda da serpente com seus próprios itens alimentares e será capturada pela serpente. Espécies de serpentes de várias famílias possuem engodo caudal, como *Tropidodryas striaticeps* (COPE, 1870), *Pantherophis spiloides* (DUMÉRIL, BIBRON & DUMÉRIL, 1854) (Colubridae), *Boa constrictor* LINNAEUS, 1758 (Boidae), *Morelia viridis* (SCHLEGEL, 1872) (Pythonidae), *Acanthophis antarcticus* (SHAW, 1802) e *Acanthophis praelongus* RAMSAY, 1877 (Elapidae) (Murphy, Carpenter & Gillingham, 1978; Radcliffe, Chiszar & Smith, 1980; Chiszar, Boyer, Lee, Murphy & Radcliffe, 1990; Sazima & Puorto, 1992; Mullin, 1999; Hagman, Phillips & Shine, 2008).

Engodo caudal em Viperidae

Engodo caudal é, sem dúvida, mais comum em espécies da família Viperidae OPPEL, 1811 (Reiserer & Schuett, 2008) do que entre membros das demais famílias de serpentes. Os viperídeos formam uma família muito diversa, compreendendo 359 espécies distribuídas em três subfamílias, Azemiopinae, Crotalinae e Viperinae, e 39 gêneros (Uetz, Freed & Hošek, 2020). Alencar *et al.* (2016) investigaram a dinâmica de diversificação e relações filogenéticas dentro da família Viperidae, criando uma hipótese de filogenia molecular baseada em 11 sequências gênicas, mitocondriais e nucleares, de 264 espécies existentes, abarcando 34 dos 35 gêneros descritos até o momento. Este trabalho, a mais completa análise filogenética para a família no momento, confirmou o monofiletismo de Viperidae e suas subfamílias.

Os juvenis de algumas espécies de crotalíneos apresentam o engodo caudal como uma de suas estratégias de forrageamento, incluindo *Agkistrodon contortrix* (LINNAEUS, 1766), *A. piscivorus* (LACÉPÈDE, 1789), *A. bilineatus* GÜNTHER, 1863, *Hypnale hypnale* (MERREM, 1820) e *Atropoides nummifer* (RÜPPELL, 1845) (Neill, 1960). O engodo caudal só ocorre em ambientes onde a serpente pode se camuflar, não ocorre em lugares que sejam muito claros ou muito escuros (a serpente deve estar camuflada, porém sua cauda deve estar visível) e só aconteceria com a presença de presas visíveis (Neill, 1948, 1960).

A maioria das serpentes que apresentam engodo caudal como uma de suas estratégias apenas o fazem quando são jovens, porque perdem a conspicuidade da ponta da cauda quando atingem a idade adulta, quando a mesma se torna similar à coloração do resto do corpo (Heatwole & Davison, 1976). Contudo, engodo caudal também é encontrado em adultos de algumas espécies como *Bothrops bilineatus* (WIED-NEUWIED, 1821), *B. insularis* (AMARAL, 1921) e *Cerastes vipera* (LINNAEUS, 1758) (Greene & Campbell, 1972; Heatwole & Davison, 1976; Andrade *et al.*, 2010).

Alguns autores argumentam que a perda do comportamento de engodo caudal após atingir a idade adulta em algumas espécies está relacionada a mudanças ontogenéticas na dieta dessas espécies, de presas ectotérmicas para presas endotérmicas (Greene & Campbell, 1972; Heatwole & Davison, 1976). Entretanto, a persistência desse comportamento em serpentes adultas de algumas espécies pode estar relacionada ao fato de que elas não mudam o tipo de presa ingerida quando adultas (Greene & Campbell, 1972; Heatwole & Davison, 1976). Além disso, muitos assumem que a presença da ponta da cauda conspícua em espécies de serpentes deveria significar que elas também apresentam o comportamento de engodo caudal, chamando atenção para uma forte relação entre essas duas características (e.g. Neill, 1960; Martins, Marques & Sazima, 2002; del Marmol, Mozaffari & Gállego, 2016).

Métodos filogenéticos comparativos em estudos ecológicos

Métodos filogenéticos comparativos, como reconstrução de caracteres ancestrais e modelos evolutivos, vêm sendo amplamente utilizados para o desenvolvimento de hipóteses sobre como traços ecológicos e/ou morfológicos evoluíram, sendo úteis, também, para analisar correlações inferidas entre estes caracteres (e. g. Alencar, Gaiarsa, & Martins, 2013; Alencar, Martins, Burin & Quental, 2017; Carvajal-Castro *et al.* 2020; Menezes & Santos, 2020). Este conjunto de métodos usa informações sobre padrões e características que vemos em espécies de animais viventes, combinadas com suas relações filogenéticas, e analisa seus putativos estados ancestrais para inferir sobre o surgimento e manutenção de características ao longo da história evolutiva.

O engodo caudal é um comportamento complexo e alguns autores (e.g. Neill, 1960; Martins *et al.*, 2002; del Marmol *et al.*, 2016) argumentam que ele ocorre concomitante à mudança ontogenética na dieta e à presença de ponta da cauda conspícua. Neste trabalho, eu pretendo investigar se realmente existe relação entre esses três caracteres, visto que eles são recorrentes na família Viperidae. Para tal, utilizei a reconstrução dos estados ancestrais dos três caracteres em viperídeos, buscando a origem desses traços, bem como sua permanência em determinados grupos. Além disso, aferi o sinal filogenético de tais caracteres para analisar se sua presença está mais relacionada ao histórico evolutivo dos viperídeos (e, portanto, herdados de um ancestral comum) ou a restrições ecológicas (e, por isso, surgindo diversas vezes ao longo da evolução deste grupo).

A minha dissertação testa pela primeira vez o sinal filogenético e a correlação de tais caracteres. Visando a publicação do mesmo, apresento o manuscrito escrito em língua inglesa e formatado segundo as normas do periódico Journal of Animal Ecology (Fator de Impacto 4.55, Qualis A1 para Biodiversidade).

Journal of Animal Ecology

Do conspicuous tails and dietary shifts indicate luring behavior in vipers?

ABSTRACT

Aggressive mimicry is an ambush strategy that is present in various animal taxa. There are several examples of aggressive mimicry throughout the animal kingdom, one of which happens when the predator mimics food items of an eventual prey to attract it. Snakes present numerous feeding strategies being either active or sit-and-wait foragers. Caudal luring is the most common form of aggressive mimicry among snakes, especially in the Viperidae family. Caudal luring is the attraction of prey that feeds on worm-like invertebrates by a cryptically colored snake that waves a conspicuous tail tip. It is often performed by juvenile snakes that also present ontogenetic shifts in diet from ectothermic to endothermic prey. Several authors assumed that the presence of caudal luring (CL) is correlated to conspicuous tail tips (CTT) and ontogenetic shifts in the diet (OSD), but that correlation was never tested. Herein, I investigated the pattern of origin and persistence of CL, CTT, and OSD along Viperidae evolution, measuring their phylogenetic signal as well as testing if there is indeed a correlation between these characters. I searched for information about the presence or absence of CL, CTT, and OSD in the scientific literature for 263 species of viperids found in Alencar *et al.* (2016) phylogeny, and assembled it in a data matrix. I also used websites of citizen science and scientific popularization that had reliable species identification. I used Phylogenetic comparative methods to measure the phylogenetic signal of the three characters, to test if there is a correlation between each pair of characters, as well as to reconstruct the ancestral character state for the family Viperidae using parsimony and maximum likelihood. I found that all characters have a strong phylogenetic signal, which means that the evolution of the characters is more correlated to the shared evolution inside Viperidae than to ecological constraints. Also, I found there is significant correlation between all the pairs of characters, which corroborates suggestions made previously in the literature. Maximum likelihood reconstruction returned that the ancestor of Viperidae presented all three characters, while the parsimony approach indicated the viperid ancestor having CL and CTT but without OSD. Studies that bring further information on the natural history of viperid snakes should contribute to enrich and complement the knowledge on Viperid evolution.

Keywords: Ancestral character reconstruction, ontogenetic shifts in diet, conspicuous tail tips, phylogenetic comparative methods, aggressive mimicry.

INTRODUCTION

Aggressive mimicry and luring as feeding strategies

Predators thoughout the animal kingdom present various strategies to hunt and capture their prey (Glaudas & Alexander, 2016). Aggressive mimicry is an example of foraging strategy displayed by some predators (Greene, 1997), which happens when the predator avoids detection by their prey because it resembles the prey itself, or something neutral or even beneficial to its prey (Ramya, Kumar, Keerthi, Srinivasa & Ramesh, 2017). This kind of strategy is advantageous because, when the prey is fooled by the signals made by its predator, the predator is benefited (Glaudas & Alexander, 2016).

Aggressive mimicry is widely distributed across several taxa. Among birds, great grey shrikes (*Lanius excubitor* LINNAEUS, 1758) attract small passerine prey by imitating their songs during winter, a form of aggressive mimicry that is also called acoustical luring (Atkinson, 1997). Another example of acoustic mimicry is when the orthopteran katydid (*Chlorobalius leucoviridis* TEPPER, 1896) mimics the acoustic signals made by cicadas of the Tribe Cicadettini to attract male cicadas that are looking for receptive females (Marshall & Hill, 2009). Assassin bugs (*Stenolemus bituberus* STÅL, 1874) create vibrations in spider webs to lure and capture them as prey (Wignall & Taylor, 2011). Bioluminescence is also known to be used as a lure by many aquatic animals including anglerfishes, squids, and octopuses (Haddock, Moline & Case, 2010).

An interesting form of aggressive mimicry is when the predator lures its prey by mimicking food items used by the prey (Ramya *et al.* 2017). Alligator snapping turtles present an annelid-like projection in its tongue used to attract fish (Harrel & Stringer, 1997) and some spiders use their webs to mimic patterns and/or colors of their prey's food items (Jackson, 1992; Ramya *et al.* 2017).

Snakes are exclusively carnivorous animals (Marques, Eterovic & Sazima, 2019) and present numerous feeding strategies being either active foragers, moving around their environment searching for prey, seizing it as they are found (Lillywhite, 2014), or ambush (sit-and-wait) hunters, searching for a place with a relatively high concentration of prey, where they sit and wait for the feeding opportunity (Lillywhite, 2014). Some sit-and-wait predator snakes employ aggressive mimicry as well, for instance species that perform lingual luring behavior (attraction of prey by movements of the tongue), including *Nerodia clarkii* (BAIRD & GIRARD, 1853), *Nerodia rhombifer* (HALLOWELL, 1852), *Nerodia sipedon* (LINNAEUS, 1758), *Thamnophis atratus* KENNICOTT, 1860, *Thamnodynastes strigatus* (GÜNTHER, 1858) and *Bitis arietans* MERREM, 1820 (Mario-da-Rosa *et al.* 2020).

Caudal luring (CL) is a common form of aggressive mimicry among snakes. This hunting strategy consists in the attraction of prey that feeds on worm-like invertebrates by a cryptically colored snake that waves a conspicuous tail tip (CTT) (Heatwole & Davison, 1976; Reiserer & Schuett, 2008). If successful, the prey will mistake the snake's tail tip for its own prey and get captured by the snake. Furthermore, it is a way to take part actively in foraging without the actual chase, thus minimizing energy expenses and exposure to predators (Reiserer, 2002). Snake species of numerous families have been reported to show caudal luring, such as *Tropidodryas striaticeps* (COPE, 1870), *Pantherophis spiloides* (DUMÉRIL, BIBRON & DUMÉRIL, 1854) (Colubridae), *Boa constrictor* LINNAEUS, 1758 (Boidae), *Morelia viridis* (SCHLEGEL, 1872) (Pythonidae), *Acanthophis antarcticus* (SHAW, 1802), and *Acanthophis praelongus* RAMSAY, 1877 (Elapidae) (Murphy, Carpenter & Gillingham, 1978; Radcliffe, Chiszar & Smith, 1980; Chiszar, Boyer, Lee, Murphy & Radcliffe, 1990; Sazima & Puorto, 1992; Mullin, 1999; Hagman, Phillips & Shine, 2008).

Caudal luring in Viperidae

Caudal luring is, by far, most common among representatives of Viperidae OPPEL, 1811 (Reiserer & Schuett, 2008). Viperids form a remarkably diverse snake family, comprising 365 species distributed in 35 genera, allocated in 3 subfamilies, Azemiopinae, Crotalinae, and Viperinae (Uetz, Freed & Hošek, 2020). Alencar *et al.* (2016) investigated the diversification dynamics and phylogenetic relationships within the Viperidae family, creating a molecular phylogenetic hypothesis based on 11 mitochondrial and nuclear gene sequences, from 263 existent species, comprising 34 of the 35 genera described at the time. Their work resulted in the most comprehensive phylogenetic analysis for the family to date, corroborating the monophyly of Viperidae and its subfamilies.

Juveniles of some crotaline species that present caudal luring as one of their feeding strategies, include *Agkistrodon contortrix* (LINNAEUS, 1766), *A. piscivorus*

(LACÉPÈDE, 1789), *A. bilineatus* GÜNTHER, 1863, *Hypnale hypnale* (MERREM, 1820) and *Atropoides nummifer* (RÜPPELL, 1845) (Neill, 1960). It has been suggested that caudal luring would only occur in an environment where the snake could camouflage itself, since the snake's body needs to be camouflaged, while its tail tip must be visible; and the snake only uses this strategy when visible prey (in that case, frogs) are present (Neill, 1948, 1960).

Most records indicate that only juveniles of most snake species have caudal luring as one of their strategies, because they lose the conspicuous tail tip when they reach adult age, as the tail becomes similar to the rest of their body (Heatwole & Davison, 1976). However, caudal luring is also reported in adults in some species, such as *Bothrops bilineatus* (WIED-NEUWIED, 1821), *B. insularis* (AMARAL, 1921), and *Cerastes vipera* (LINNAEUS, 1758) (Greene & Campbell, 1972; Heatwole & Davison, 1976; Andrade *et al.*, 2010).

Several authors assumed that the presence of a conspicuous tail tip is correlated to the caudal luring behavior, bringing attention to a close relationship between these two characters (*e.g.* Neill, 1960; Martins, Marques & Sazima, 2002; del Marmol, Mozaffari & Gállego, 2016), arguing that the loss of caudal luring behavior in adulthood might be related to ontogenetic shifts in their diet (OSD), from ectothermic to endothermic prey (Greene & Campbell, 1972; Heatwole & Davison, 1976). Conversely, the persistence of caudal luring in some adult snakes might be related to the absence of OSD in these species (Greene & Campbell, 1972; Heatwole & Davison, 1976).

Comparative phylogenetic methods in ecological studies

Comparative phylogenetic methods, such as ancestral state reconstructions and evolutionary models, are often used to develop hypotheses on how ecological and/or morphological traits evolved, also being useful to access putative correlations between those traits (*e. g.* Alencar, Gaiarsa, & Martins, 2013; Alencar, Martins, Burin & Quental, 2017; Carvajal-Castro *et al.* 2020; Menezes & Santos, 2020). These methods can, based on a known phylogeny, suggest the plesiomorphic condition of some characters, allowing discussions on patterns of trait modification along a lineage evolution.

My main objective is to investigate the pattern of origin and persistence of caudal luring behavior along Viperidae evolution, considering both its phylogenetic signal and possible constraints to its occurrence, especially regarding the presence of ontogenetic shifts on diet and conspicuous tail tip. Thus, I intend to test the correlation between those three characters, proposed anecdotally by several authors (*e.g.* Neill, 1960; Martins *et al.*, 2002; del Marmol *et al.*, 2016), but never tested using phylogenetic and statistical approaches.

MATERIAL AND METHODS

Data Collection

I searched the scientific literature for information concerning the presence or absence of caudal luring behavior; conspicuous tail tip, and ontogenetic shift in diet for the 263 species of viperids found in Alencar *et al.* (2016) phylogeny, as well as 25 outgroup species (Table S4 in Supplementary Material). I considered as conspicuous tail tip any tail which its shape and/or coloration was remarkably different than the snake's body, which was cryptic for camouflaging. Regarding rattlesnakes, I did not consider the rattle as conspicuous, only the coloration of the tail itself. I only considered ontogenetic shift in diet from eating mainly ectothermic prey when juveniles to eating mainly endothermic prey while adults. I used Google Scholar and The Reptile Database (Uetz, Freed & Hošek, 2020) to find results of academic content specifically, as well as Google for general sources of information.

The searched keywords were the species' scientific name and/or its common names combined with character keywords (behavior, diet, caudal luring, feeding behavior, juvenile, ecology, natural history). The search was conducted in English, Portuguese, Spanish, and French, among other languages according to a species country of occurrence. Due to the scarcity of results for some species, when searching for the presence of conspicuous tail tips, I also decided to use pictures found in citizen science and scientific popularization websites with reliable species identification (e.g. iNaturalist).

I assembled this information in a discrete data matrix, coding the presence or absence of CL, CTT, and OSD. I included only reliable data, obtained from published scientific articles or, when acquired from citizen science and popularization websites, only data referenced to scientific literature. A massive effort was made on separating conjectural from actual evidence about the characters of interest, as explained above. On caudal luring, I disregarded mere assumptions and suppositions made concerning the presence of this behavior in a given species (e.g., Neill, 1960; Martins *et al.*, 2002; del Marmol *et al.*, 2016), taking into consideration only information from studies about the natural history, or where the behavior was recorded and described, as well as direct observations (videos, personal communication with authors) that reported caudal luring. Regarding ontogenetic shift in diet, I did not include studies that did not specify clearly which prey was captured by adults and those captured by juveniles. Concerning the conspicuous tail tips of the snakes, when a reliable species identification was not found at the source of the image, I contacted the author to verify how the snake was identified or contacted group specialists to confirm its identification. Finally, the data matrix presents species of the Viperidae family for which information was found about at least one of the three characters.

Phylogeny

I conducted all comparative analyses using the Viperidae phylogeny of Alencar *et al.* (2016), trimmed to the taxa presented in the data matrix. This phylogeny is currently the most comprehensive phylogenetic hypothesis for the family, with 263 species distributed in 34 of the 35 Viperidae genera known at the time. I pruned the Alencar *et al.* (2016) tree and my dataset to have correspondence for the following comparative analyses. I used 20 species as outgroup in the comparative analyses, which were also obtained from Alencar *et al.* (2016) phylogeny.

Phylogenetic Comparative Analyses

Ancestral character reconstruction and evolutionary models

I used two methods of character optimization and ancestral reconstruction for each character. Fitch parsimony algorithm (Fitch, 1971), with accelerated transformation optimization (ACCTRAN), as suggested by de Pinna (1991), was conducted on Winclada software (Nixon, 2002), since it takes into account uncertainties related to missing information about one or two of the three traits studied while reconstructing the ancestral states of the characters.

Additionally, I reconstructed the ancestral state using maximum likelihood (ML), with a reduced matrix which presented only complete information regarding each of the three characters, using R (R Core Team, 2019), in RStudio (RStudio Team, 2019). To perform the ancestral character reconstruction, I tested different models for state transition rates, using the *fitDiscrete* function of the "geiger" R-package (Harmon *et al.*, 2008). I tested the "Equal Rates model" (ER) as well as the "All-Rates- Different model" (ARD), the first assuming that all transitions between trait states occur at the same rate (Pagel, 1994; Lewis, 2001) and the latter assuming that all transitions occur at different rates (Paradis, Claude & Strimmer, 2004). Those tests were performed under a Pagel's lambda transformation (see more in the next section), and I opted for the model with the best scores for AICc and log-likelihood, using a chi-squared ratio test (Carvajal-Castro *et al.* 2020).

The character reconstructions were performed with the best-fitted model for each character, using the *ace* function of the R-package "ape" (v. 5.3; Paradis & Schliep 2018). This function estimates the ancestral states of the characters studied employing maximum likelihood (in case of discrete characters), as well as the associated uncertainty (Paradis & Schliep 2018). The likelihood values were calculated with a joint estimation procedure (further discussed at Felsenstein, 2004), which is faster than stochastic mapping while being similarly accurate (Paradis & Schliep, 2018). The results were plotted in the trimmed tree via the *plotTree* function of "phytools" (v. 0.7.20; Revell, 2012) R-package, as well as the functions *nodelabels* and *tiplabels* from the "ape" package. The nodes present the empirical Bayesian posterior probabilities, in which the higher the value of likelihood, the higher is the probability of the character having that ancestral state.

Phylogenetic signal

The phylogenetic signal is a measurement of non-independence among species trait values because of their phylogenetic relatedness (Felsenstein, 1985). Therefore, is the tendency of related species to resemble each other more than species drawn at random from the same tree (Blomberg & Garland Jr., 2002). A variety of indices has been proposed to measure and test for phylogenetic signal, but in the present work, I used Pagel's statistic lambda (λ) (Pagel, 1997,1999).

Pagel's λ assumes a Brownian Motion model of trait evolution (*i.e.* the variance in the distribution of trait values is directly proportional to branch length) (Münkemüller *et al.*, 2012), with indices close to zero indicating phylogenetic independence for that trait, while values close to one indicate the trait is distributed as expected under a Brownian Motion evolutionary model (Pagel, 1999). Therefore, λ is the transformation of the phylogeny that ensures the best fit of trait data to a Brownian Motion model. I chose Pagel's λ because this index is less susceptible to the number of analyzed species (Münkemüller *et al*., 2012), and can be implemented for discrete binary datasets. The phylogenetic signal was measured for each character within the best-fitted model for state transition rates in R, with the *fitDiscrete* function of the "geiger" R-package.

Correlation analyses between discrete traits

To measure the strength of the relationships between caudal luring, ontogenetic shifts in diet, and conspicuous tail tips, given the phylogenetic relationships of Viperidae species, I performed a Pagel's fitting test (1994) method for the correlated evolution of two binary characters. This is different from the simple statistic method of correlation analysis because it considers the non-independence of the samples studied, in this case, the species, due to kinship. Pagel's (1994) method for correlation test uses the information on phylogenetic trees' branch lengths, developing estimates of discrete character rates of change, then tests the hypothesis of correlated evolution without the reconstructions of the ancestral character states.

The *fitPagel* function of the "phytools" R-package tests both dependent and independent models of evolution for a pair of traits, and returns the log-likelihood and AICc values of those models, which are used in a chi-squared likelihood-ratio, with 95% of confidence. If the difference between the dependent and independent models is significant, the more complex model is chosen, and we assume the analyzed characters are correlated. I ran the *fitPagel* function for the investigated characters arranged in pairs (caudal luring-conspicuous tail, caudal luring-ontogenetic shift in diet, and so on) using the previously decided model for the characters' evolution (ER or ARD). When the two analyzed traits had different best-fitted models, I chose the most complex model to run the analyses, since one of the traits was not well explained by the simplest model (ER). The analysis demands a complete dataset, so I included only species for which I had information about both analyzed characters. Then, I presented the reconstruction plots with the reduced dataset for each pair of characters, mirrored, to facilitate the visualization of the correlation analyses results.

RESULTS

From the 263 Viperidae species investigated, I found information regarding at least one character on 220 species, as well as for 20 of the 25 outgroup species studied, resulting in 240 species (83%) in total (Figure 1). The character codification according to the literature revision is presented in a data matrix (see Table S4 at supplementary material). From those 240 species, 78 had available information about caudal luring (48 “Yes” and 30 “No”), 212 about conspicuous tail tip (163 “Yes” and 49 “No”), and 163 about ontogenetic shift in diet (88 “Yes” and 75 “No”). Only 62 species have available information for all three characters. The majority of the information is regarding Crotalinae species, adding up to 157 species (65% out of the total 240 species), while only 62 species (26%) are from the Viperinae subfamily. I also found information on one of the two species of Azemiopinae known so far.

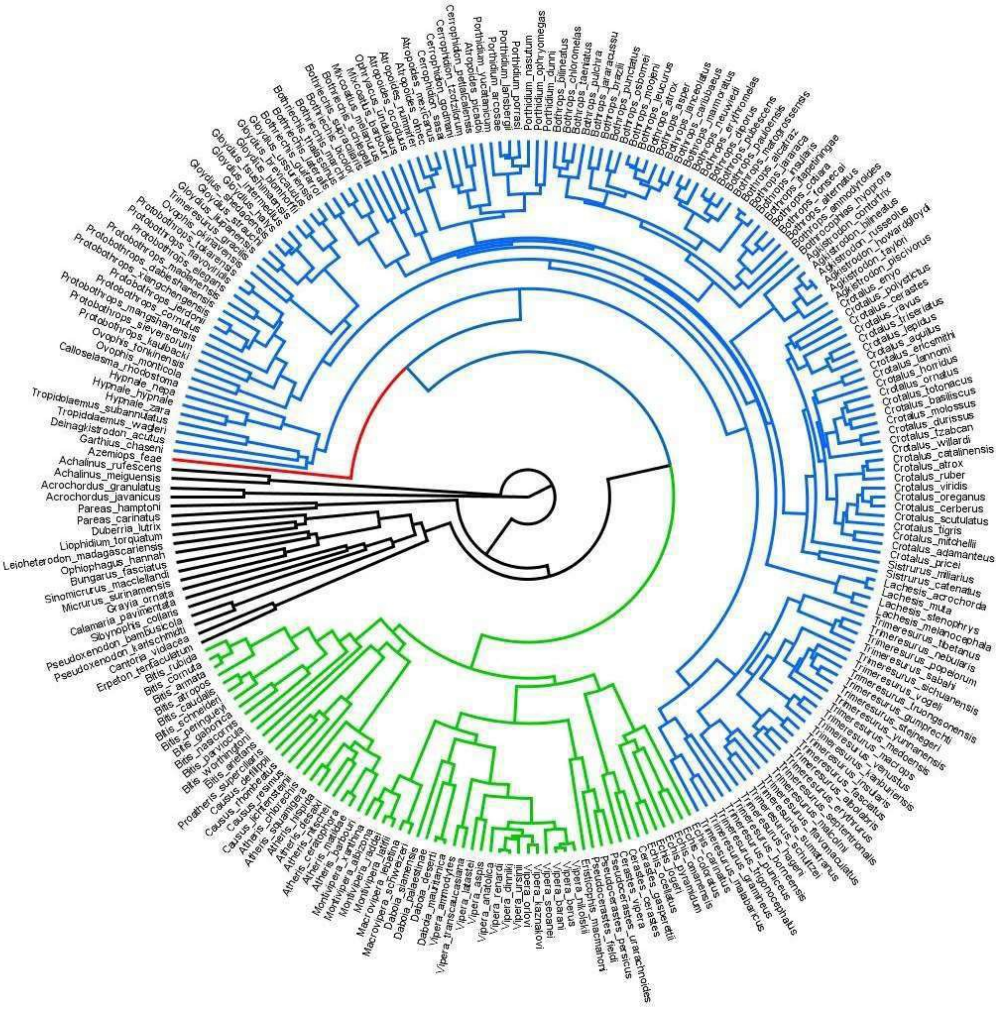


Figure 1. Phylogenetic tree for the 240 species of Viperidae, taken from Alencar *et al.* 2016, analyzed herein. Blue: Crotalinae species. Green: Viperinae species. Red: Azemiopinae species. Black: Outgroup species.

Ancestral State Reconstruction

Caudal luring

The parsimony reconstruction for the entire dataset (240 species), with ACCTRAN optimization, suggests that the Viperidae ancestor presented caudal luring behavior, which appears at the Viperidae base, while almost none of the outgroup species had caudal luring, except for *Acrochordus javanicus* (Figure 2). The reconstruction also points out that caudal luring was lost at least ten times during the Viperidae evolution and reappeared four times. The ACCTRAN optimization also indicates the most parsimonious ancestral character state for several genera that lacked information at the terminal taxa (Fig. 2).

Among the species which lost this behavior, I highlight clades such as the genus *Causus* + *Proatheris superciliaris*, the genus *Echis*, the clade formed by *Gloydius* + *Ovophis okinavensis* + *Trimeresurus gracilis* and *Lachesis* genus, for which parsimony analysis indicate all its species lost caudal luring along its evolution. Also, *Trimeresurus* is a diverse genus in which caudal luring is currently reported for only one species, and absent for another one (See Table S4). However, the parsimony reconstruction suggests this behavior might be lost in at least half of the species of this genus. In the diverse *Crotalus* genus, parsimony reconstruction indicates that the ancestor did not present caudal luring, and that this behavior might have reappeared in at least seven species.

The reconstruction suggests the absence of caudal luring in the ancestor of the clade including several genera such as *Mixcoatlus*, *Atropoides, Cerrophidion, Porthidium, Bothrocophias*, and *Bothrops*. However, most of *Bothrops* species presents this behavior, except for the *B. alternatus* group, as well as *B. alcatraz* and *B. diporus*. The reconstruction suggests caudal luring also reappeared another time in this great clade, in the species *Porthidium nasutum*.

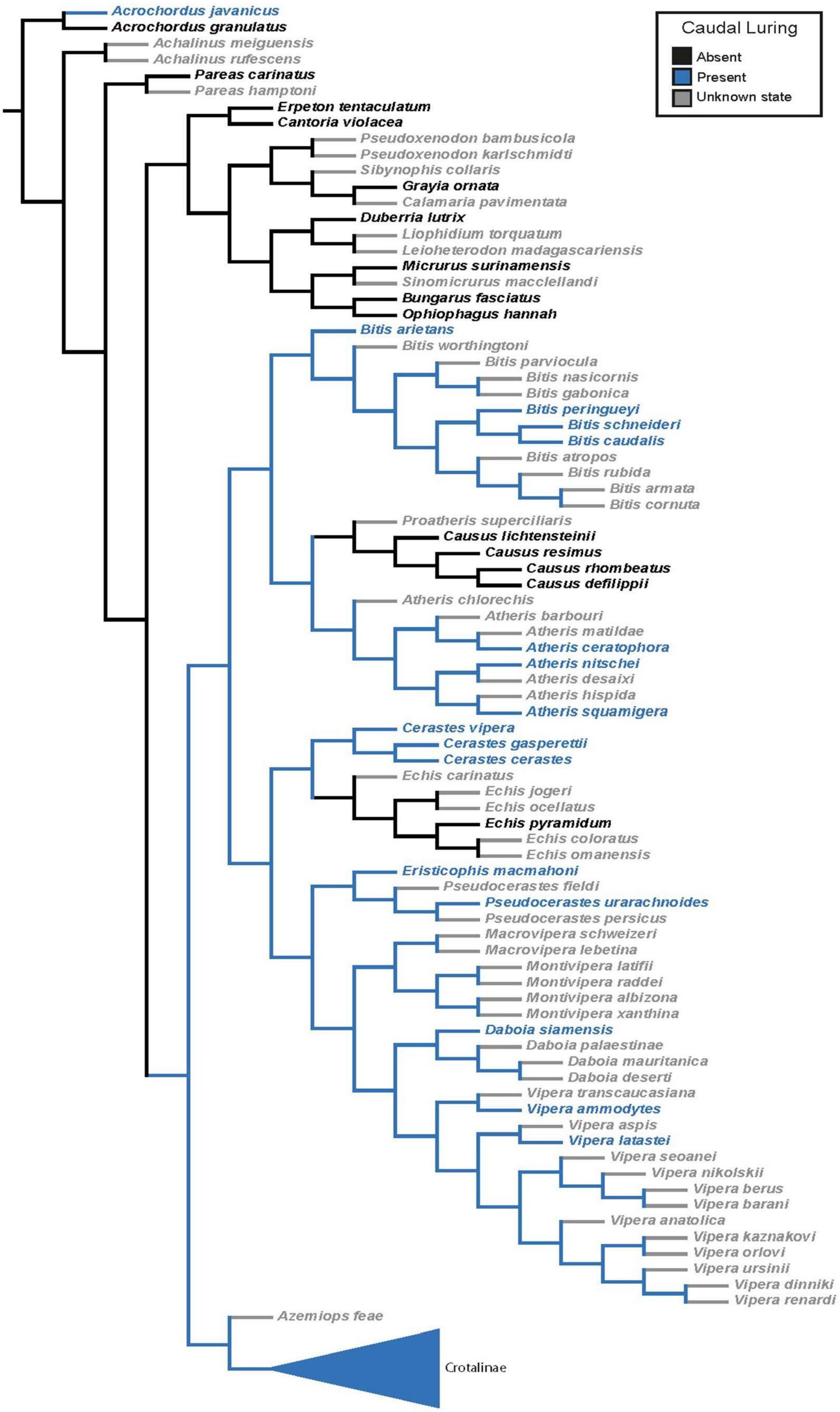


Figure 2 . Parsimony ancestral state reconstruction regarding caudal luring (CL) made using ACCTRAN optimization (to be continued in the next page).

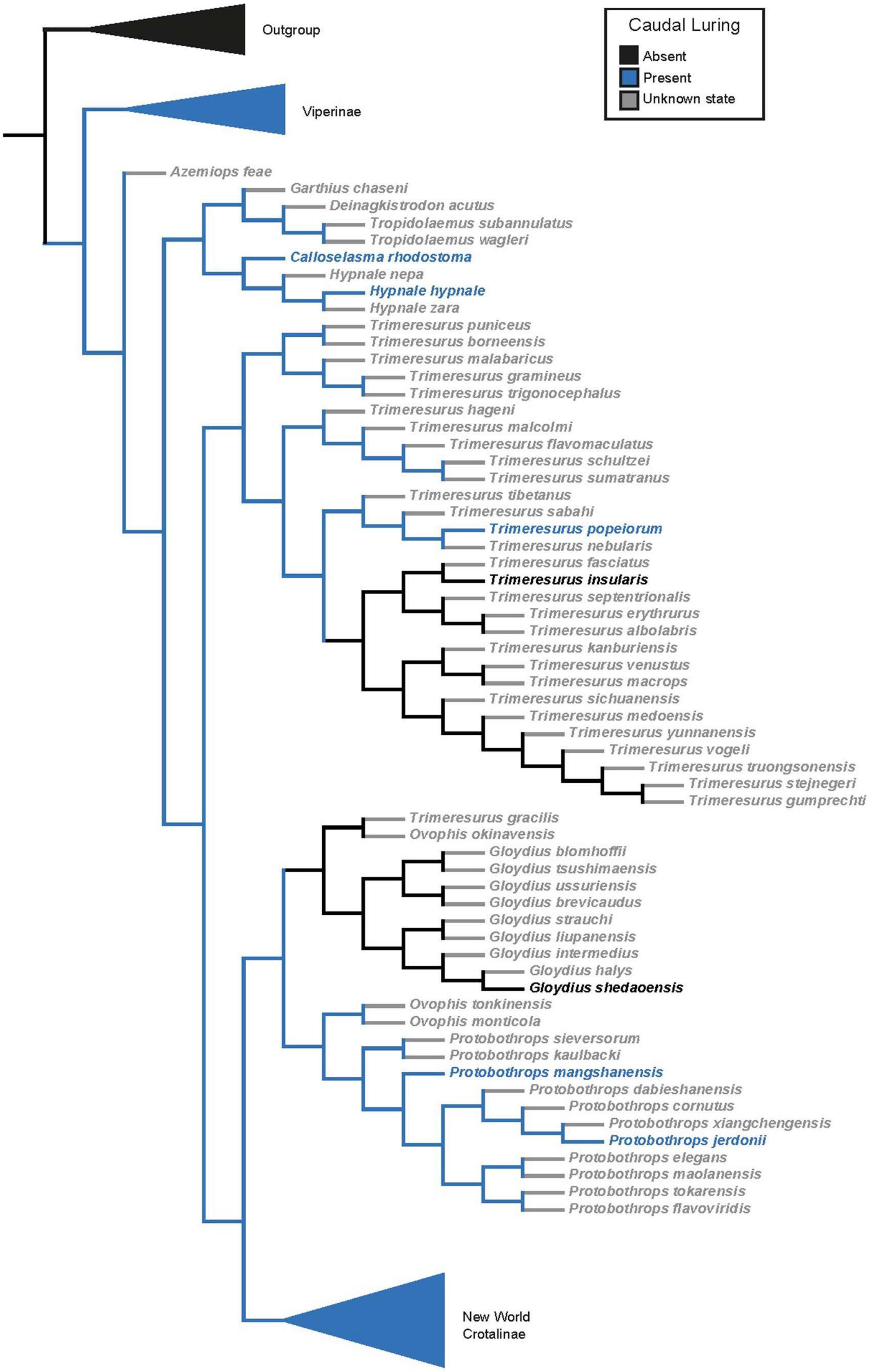


Figure 2 (continuation). Parsimony ancestral state reconstruction regarding caudal luring (CL) made using ACCTRAN optimization (to be continued in the next page).

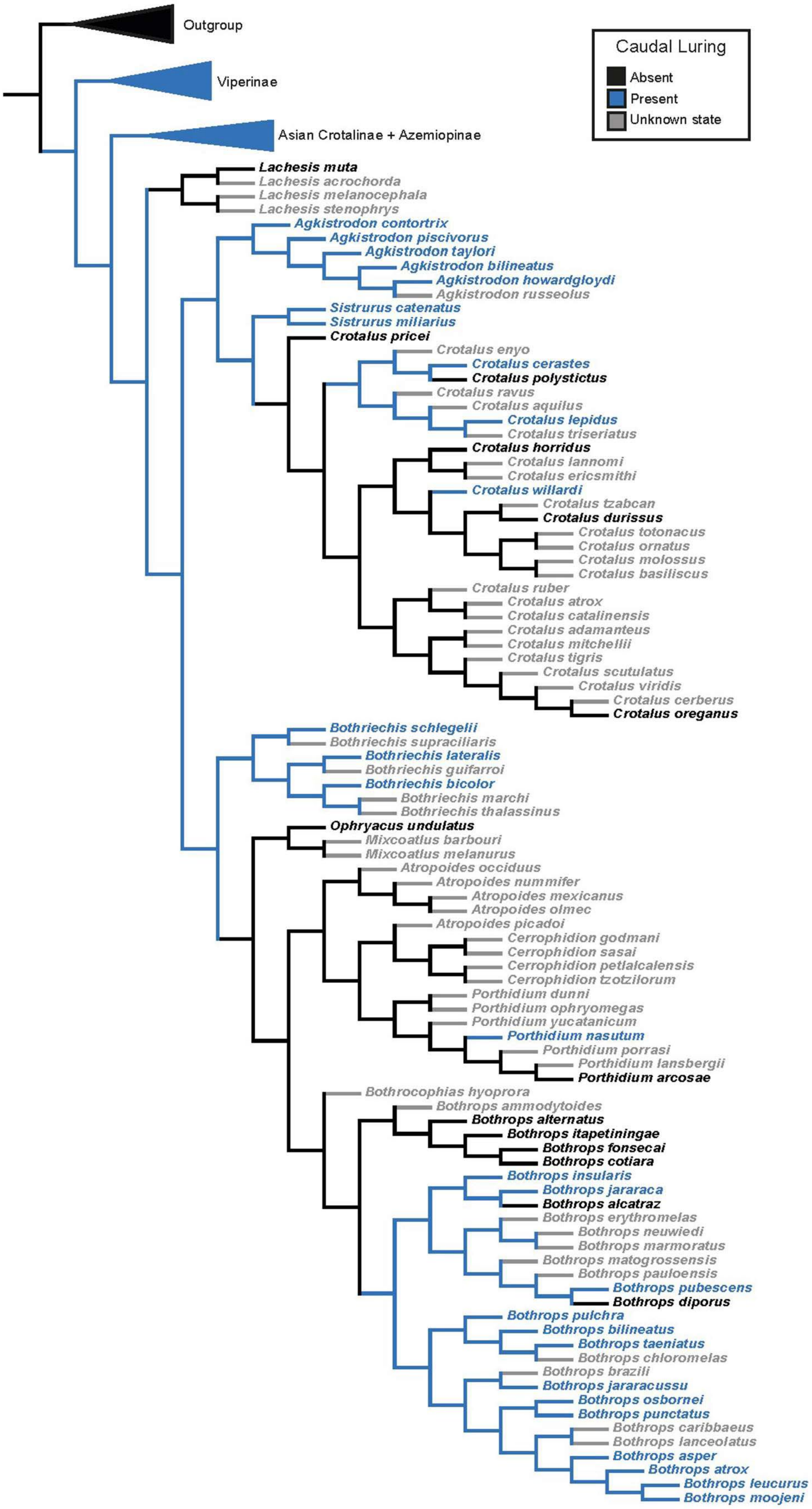


Figure 2 (continuation). Parsimony ancestral state reconstruction regarding caudal luring (CL) made using ACCTRAN optimization.

The pruned data matrix containing only the species for which I found information about caudal luring behavior presents 78 species (ten of which pertain to the outgroup). The ancestral state reconstruction of this dataset in the trimmed phylogenetic tree, made using maximum likelihood, is presented in Figure 3. The chosen model for state transition rates is the "all rates different" (ARD) model, which presented the lower Akaike value (LnL= -43.483, AICc= 93.291). The maximum likelihood reconstruction indicates that the ancestor of Viperidae probably used caudal luring as one of its hunting strategies (Fig.3; Fig. S1 of supplementary material, posterior probability = 99.5%). While almost none (nine out of ten) outgroup species present caudal luring, the behavior is recurrent in Viperidae taxa.

Within the viperids, the maximum likelihood reconstruction indicates that some clades such as the *Causus* genus and the *Bothrops alternatus* group have lost caudal luring early in their evolution, with all their species lacking this behavior. Although the *Crotalus* clade's ancestor probably displayed caudal luring (Fig.3; Fig. S1, posterior probability = 97.7%), some species lost it afterwards. The loss of caudal luring behavior appears to have occurred several times in *Crotalus* evolution, being absent, at least, in *Crotalus pricei*, *C. oreganus*, *C. durissus, C. horridus*, and *C. polystictus*. The *Bothrops* common ancestor also showed a higher probability of presenting caudal luring (Fig. 3; Fig. S1, 99%), but the species *B. alcatraz* and *B. diporus*, other than the *B. alternatus* group, also lost the behavior along their evolution.

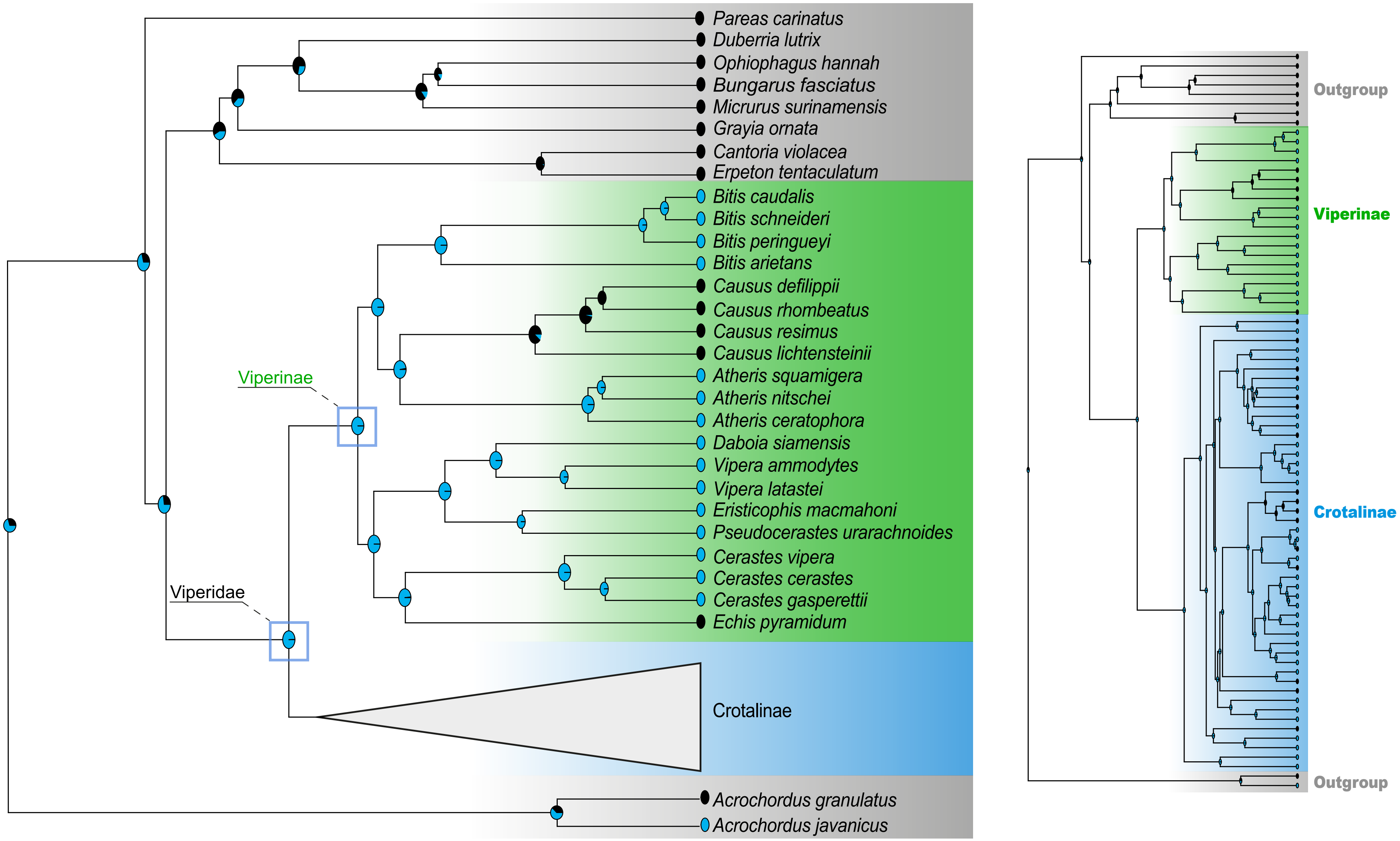


Figure 3. Ancestral state reconstruction using maximum likelihood for caudal luring (CL). The analysis was made using ARD model for state transition rates. Pie graphics at tree nodes are representing the proportional probabilities of the states. Blue: character present. Black: character absent (to be continued in the next page).

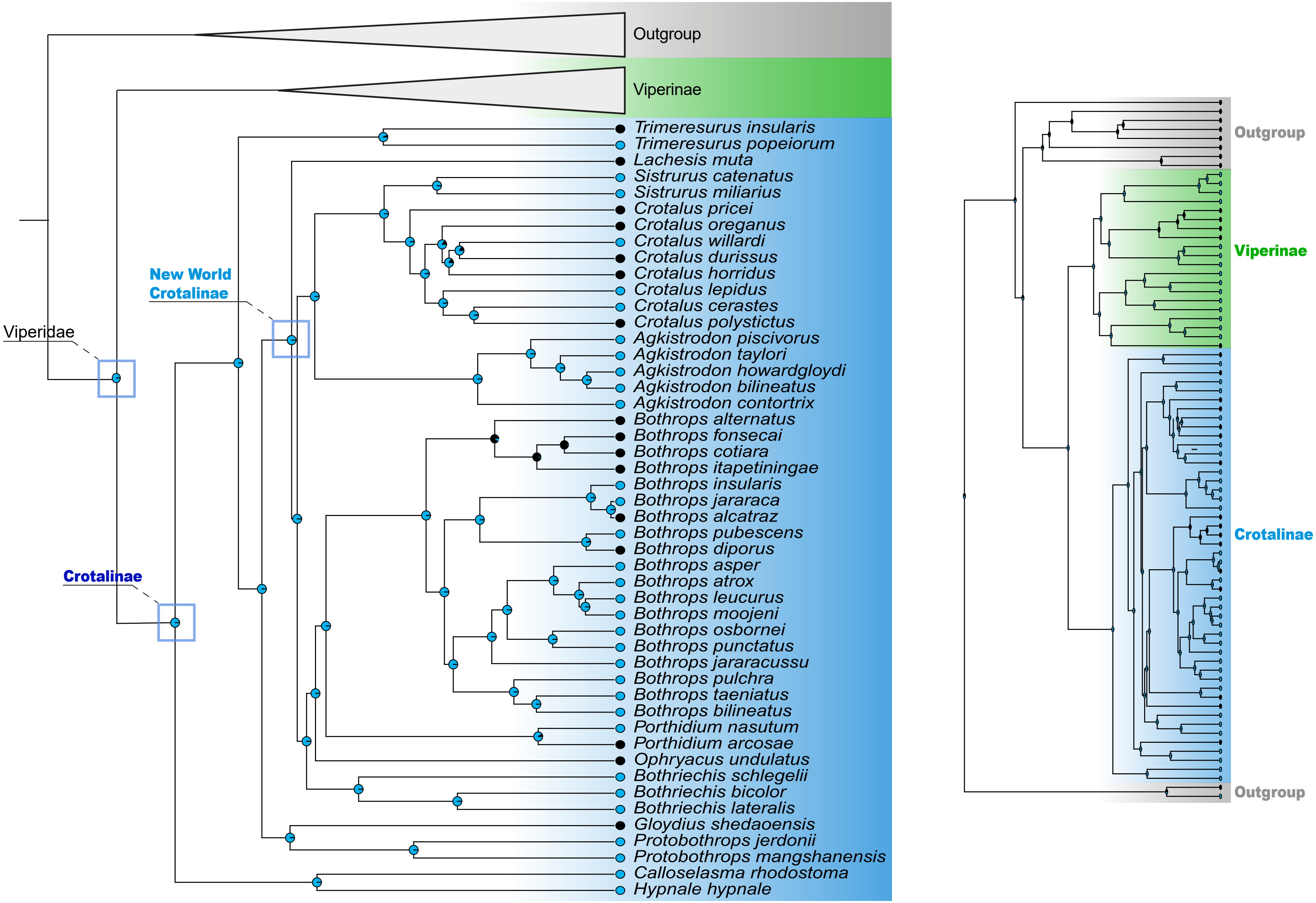


Figure 3 (continuation). Ancestral state reconstruction using maximum likelihood for caudal luring (CL). The analysis was made using ARD model for state transition rates. Pie graphics at tree nodes are representing the proportional probabilities of the states. Blue: character present. Black: character absent.

Conspicuous tail tips

The parsimony reconstruction for all 240 species, with ACCTRAN optimization, suggests that the Viperidae ancestor presented a conspicuous tail tip (Figure 6). The reconstruction indicates that this character was lost at least 26 times along the family evolution, and secondarily gained only, at best, five times. The ACCTRAN optimization indicates the most parsimonious ancestral reconstruction for several genera with missing data at some terminals (Fig. 6).

The parsimony reconstruction also indicates that this high number of losses of the conspicuous tail tip character happened several times in Viperidae evolution, but not in any major groups (i.e. diverse genera). However, this loss happened homoplastically in some species and small groups within species-rich genera, such as *Vipera, Trimeresurus, Crotalus, Bothrops,* among others (Fig. 6).

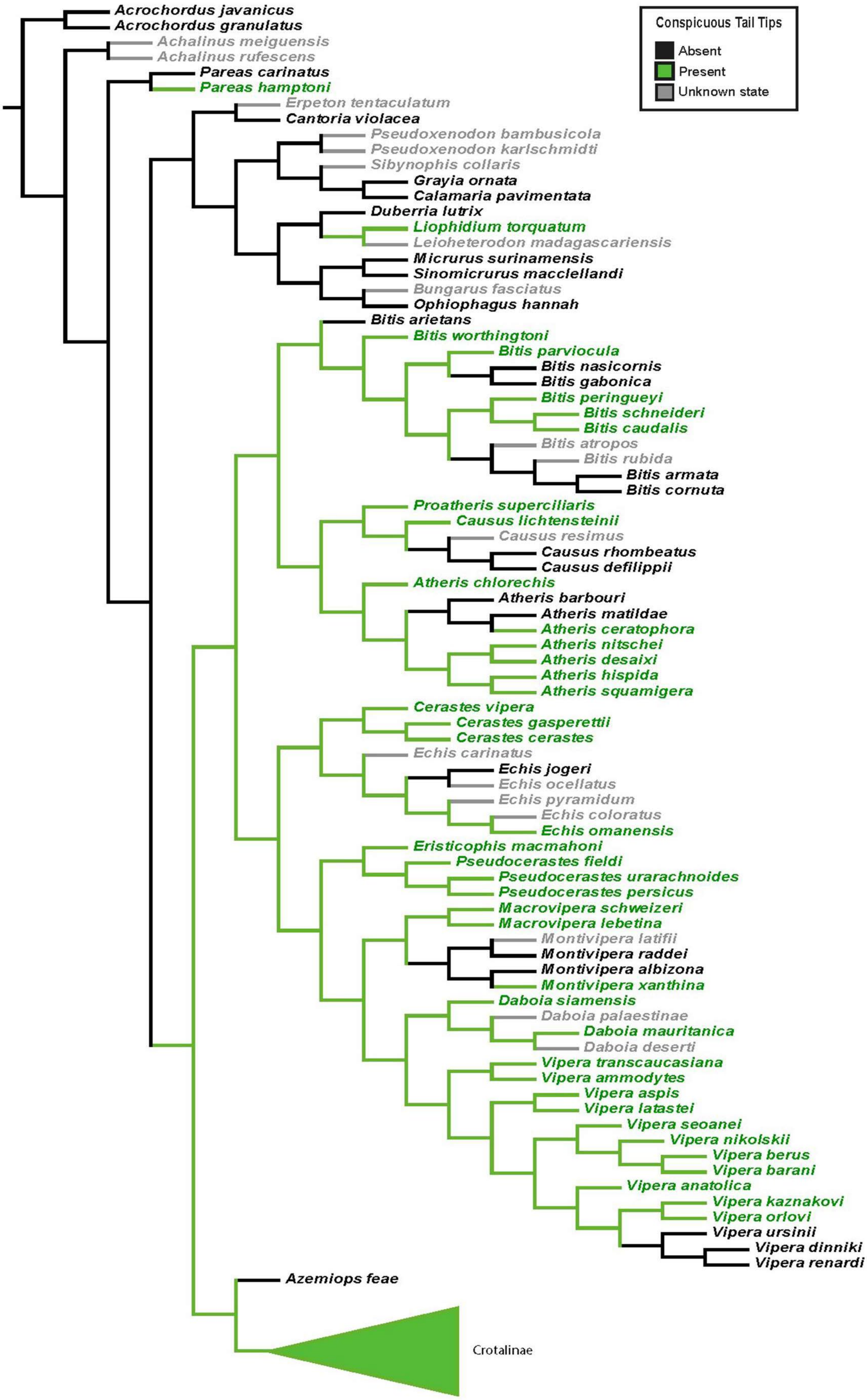


Figure 4. Parsimony ancestral state reconstruction for conspicuous tail tips (CTT) made using ACCTRAN optimization (to be continued in the next page).

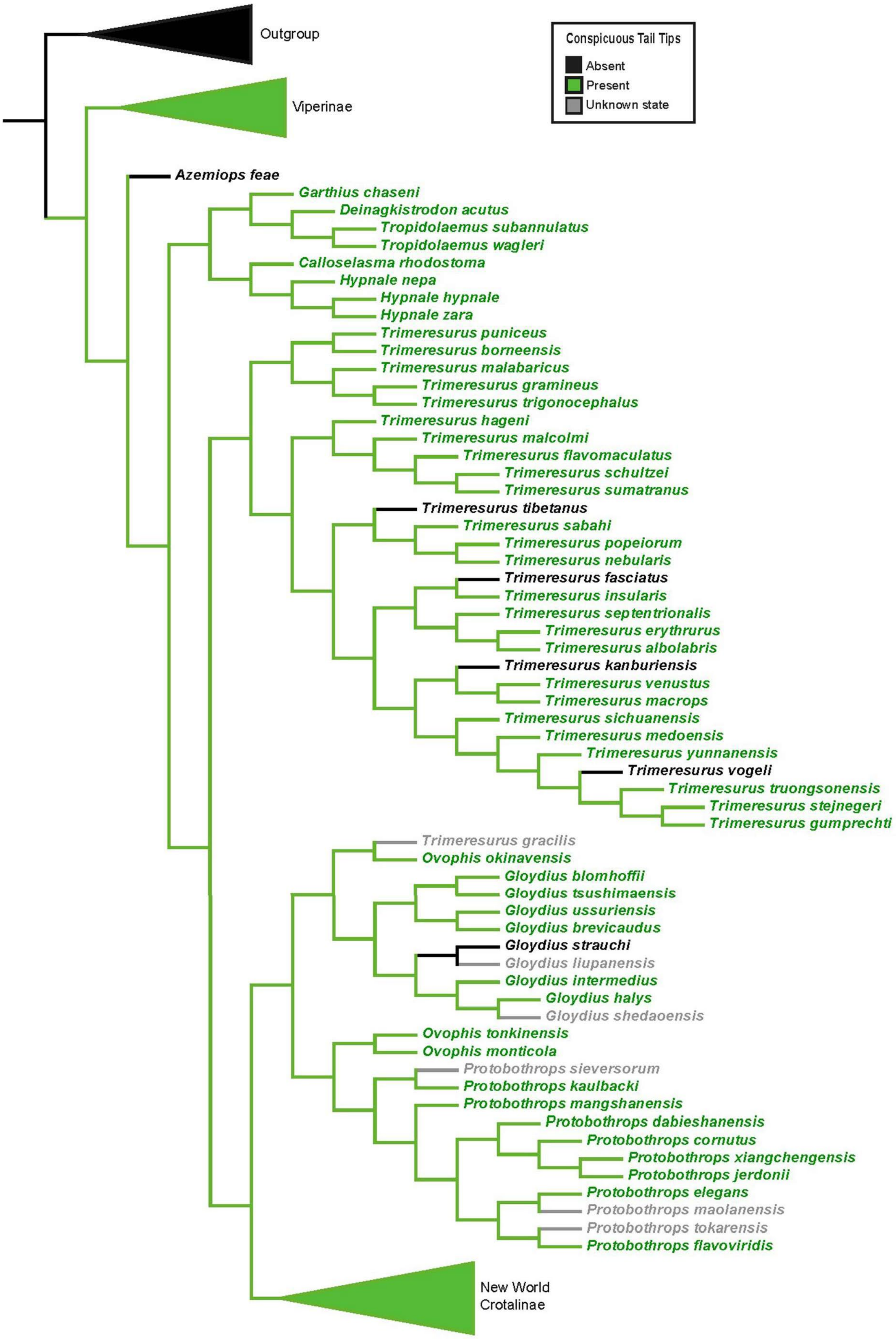


Figure 4 (continuation). Parsimony ancestral state reconstruction for conspicuous tail tips (CTT) made using ACCTRAN optimization (to be continued in the next page).

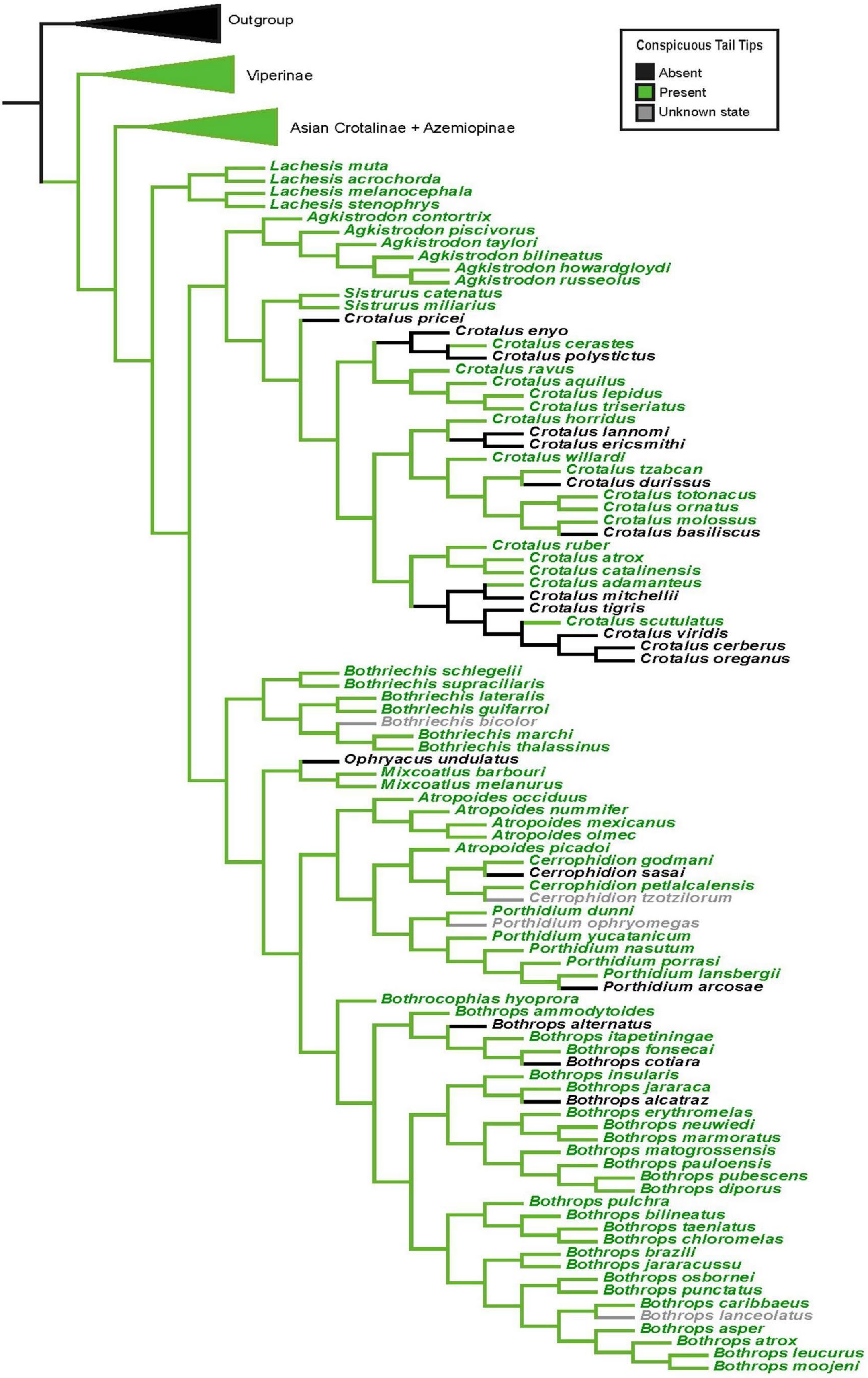


Figure 4 (continuation). Parsimony ancestral state reconstruction for conspicuous tail tips (CTT) made using ACCTRAN optimization.

For conspicuous tail tips, the pruned data matrix has 212 species (12 of which pertain to the outgroup). The ancestral state reconstruction of this dataset in the trimmed phylogenetic tree, made using maximum likelihood, is presented in Figure 7. The chosen model for state transition rates was the “Equal Rates” (ER) model, which presented the lower Akaike value (LnL= - 104.781, AICc= 213.619). The maximum likelihood reconstruction indicates that the conspicuous tail tip was probably present in the ancestor of the Viperidae family (Fig. 7; Fig. S3, 89.9%), while most of the outgroup species (10 out of 12) did not show this character. The loss of this character is scattered in several terminal taxa, having happened recently in the evolution of some Viperidae genera, including *Bitis, Atheris*, *Vipera*, *Trimeresurus*, *Gloydius, Crotalus*, *Bothrops*, and *Porthidium*.

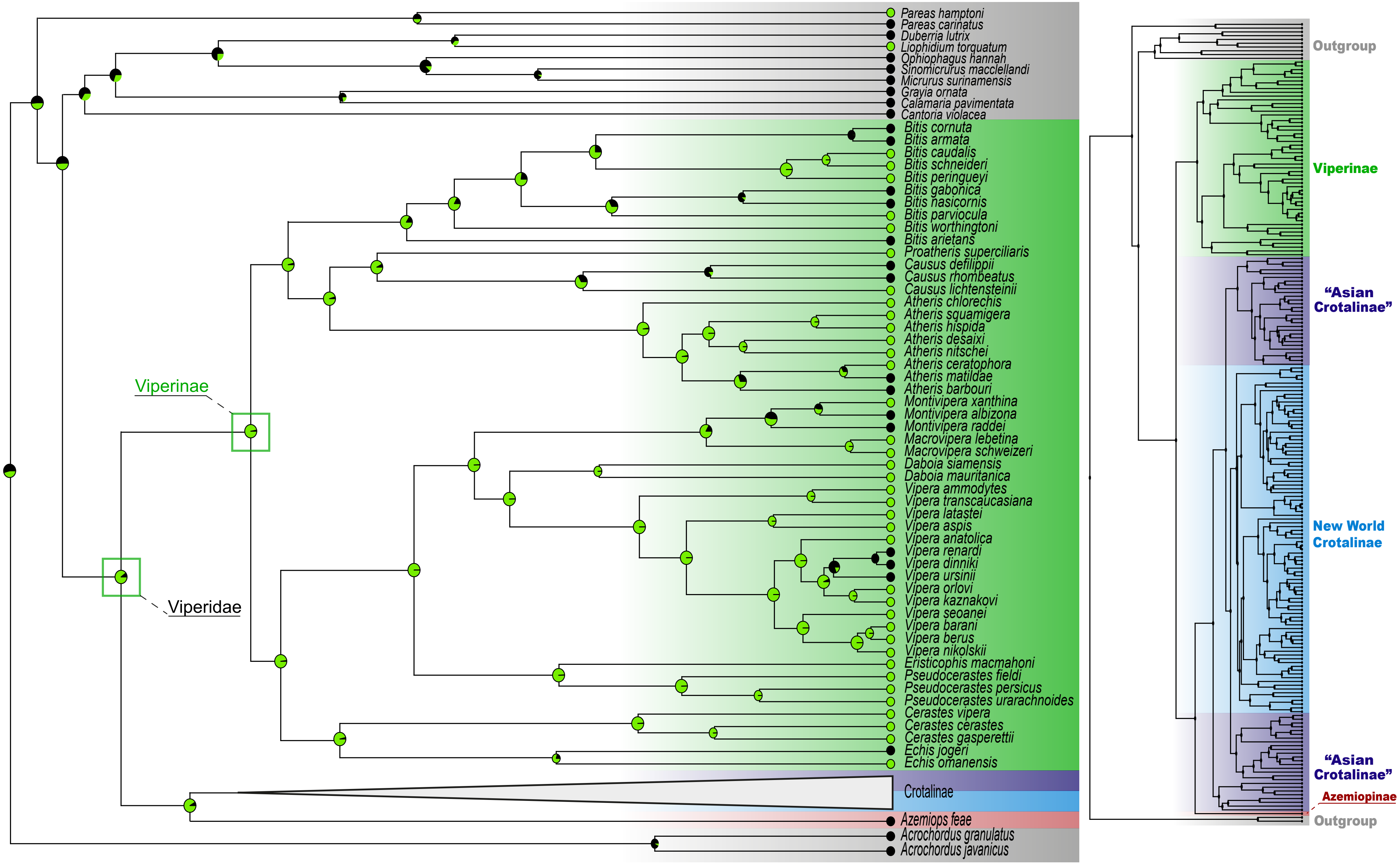


Figure 5. Ancestral state reconstruction made using maximum likelihood for conspicuous tail tips (CTT). The analysis was made using ER model for state transition rates. Pie graphics at tree nodes are representing the probabilities of the states. Green: character present. Black: character absent (to be continued in next page).

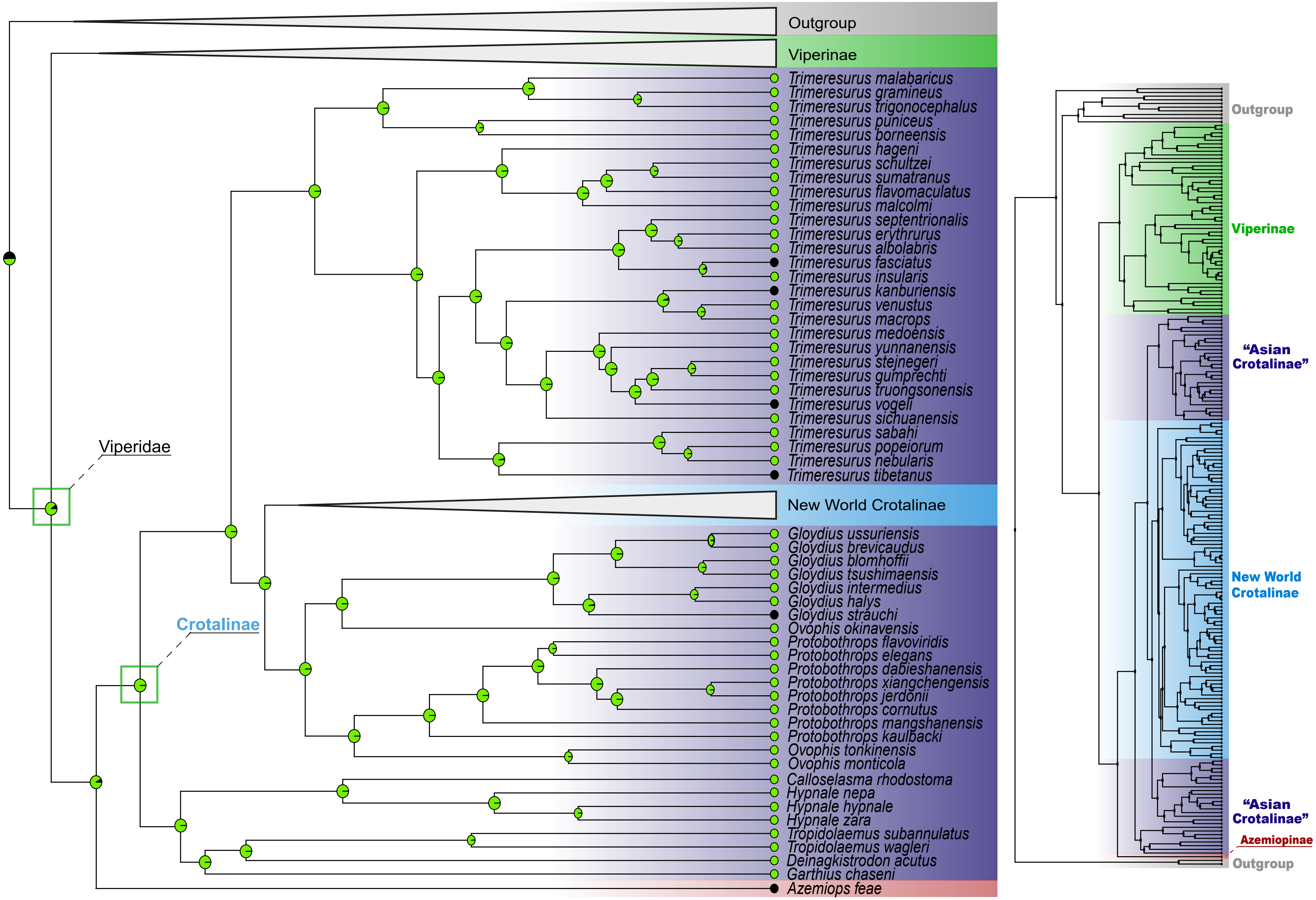


Figure 5 (continuation). Ancestral state reconstruction made using maximum likelihood for conspicuous tail tips (CTT). The analysis was made using ER model for state transition rates. Pie graphics at tree nodes are representing the probabilities of the states. Green: character present. Black: character absent (to be continued in the next page).

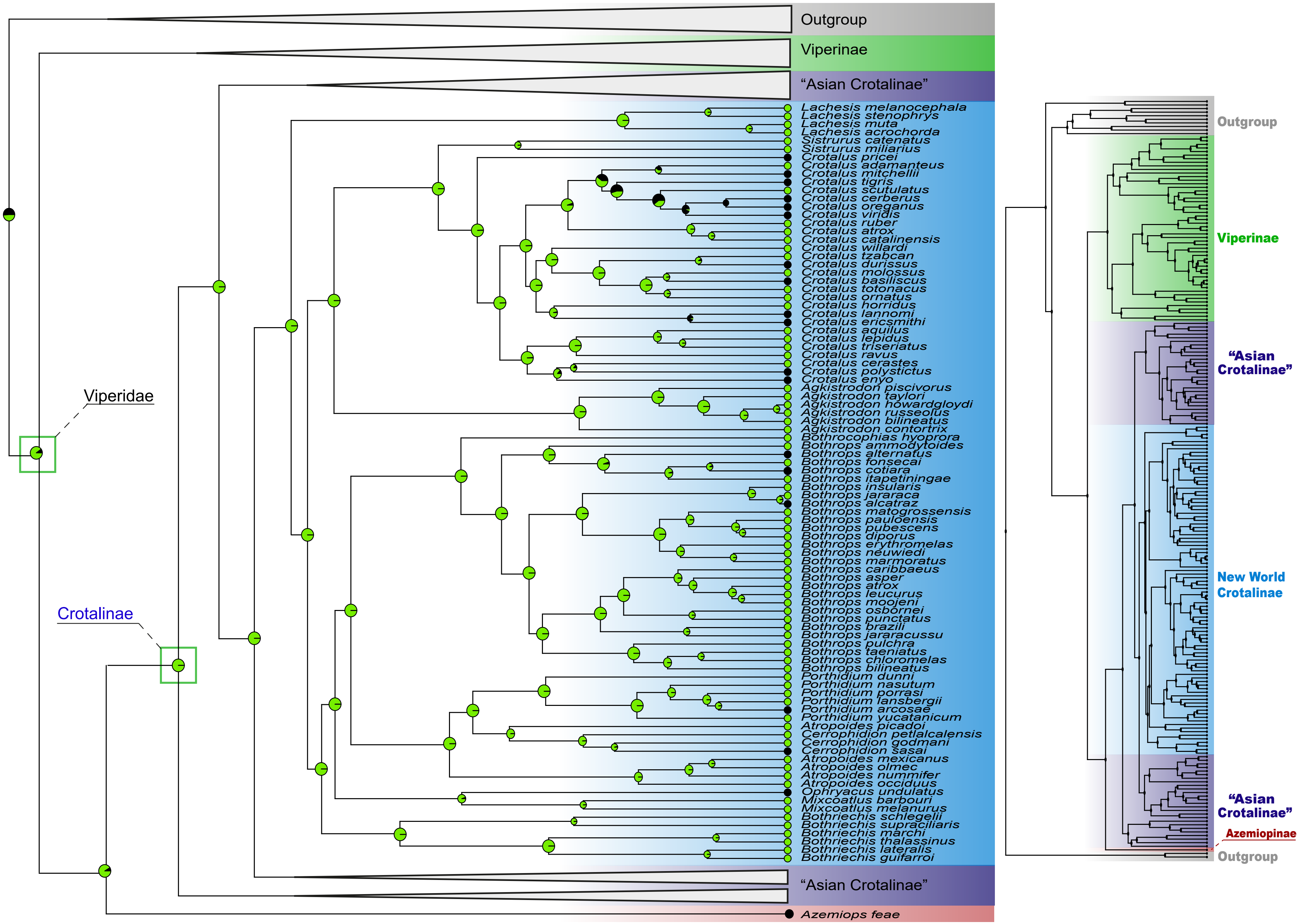


Figure 5 (continuation). Ancestral state reconstruction made using maximum likelihood for conspicuous tail tips (CTT). The analysis was made using ER model for state transition rates. Pie graphics at tree nodes are representing the probabilities of the states. Green: character present. Black: character absent .

Ontogenetic shifts in diet

The parsimony reconstruction for the entire dataset (240 species), with ACCTRAN optimization, suggests that the Viperidae ancestor did not present ontogenetic shift in diet. The reconstruction indicates that this character appeared at least 19 independent times along Viperidae evolution and was secondarily lost at least 11 times (Figure 4). The ACCTRAN optimization also indicates the most parsimonious ancestral state for several genera with missing data at some terminals (Fig. 4).

Among the species which gained this behavior, I highlight the clade that includes the genera *Macrovipera*, *Montivipera, Daboia*, and *Vipera*. The parsimony reconstruction indicates that the ontogenetic shift on diet emerged in this clade, with a secondary loss only in *Vipera anatolica*. Another parallel emergence of this condition is found for the whole *Protobothrops* genus.

Even though its ancestor did not present this character, most of the analyzed *Gloydius* species present ontogenetic shifts in diet, and the parsimony reconstruction suggests this condition arose at least twice inside *Gloydius* genus.

Through parsimony reconstruction, one of the main evolutionary events regarding the emergence of ontogenetic shift on diet in Viperidae probably happened early in the evolution of New World Crotalinae. The reconstruction suggests that this condition was originated in the monophyletic group comprising all New World Crotalinae, except for the genus *Lachesis*, and was secondarily lost in some groups, including diverse genera as *Crotalus,* several *Bothrops* groups, and some isolated species. The parsimony reconstruction indicates that ontogenetic shift on diet was absent in the *Crotalus* ancestor. However, the condition arose at least five times inside the genus, being present in 11 analyzed species. Furthermore, the ontogenetic shift in diet in the genus *Bothrops* was secondarily lost in the *B. alternatus* group, *B. neuwiedi* group (and regained in *B. pauloensis* and *B. pubescens*), in the *B. caribbaeus* + *B. lanceolatus* clade, and *B. alcatraz*.

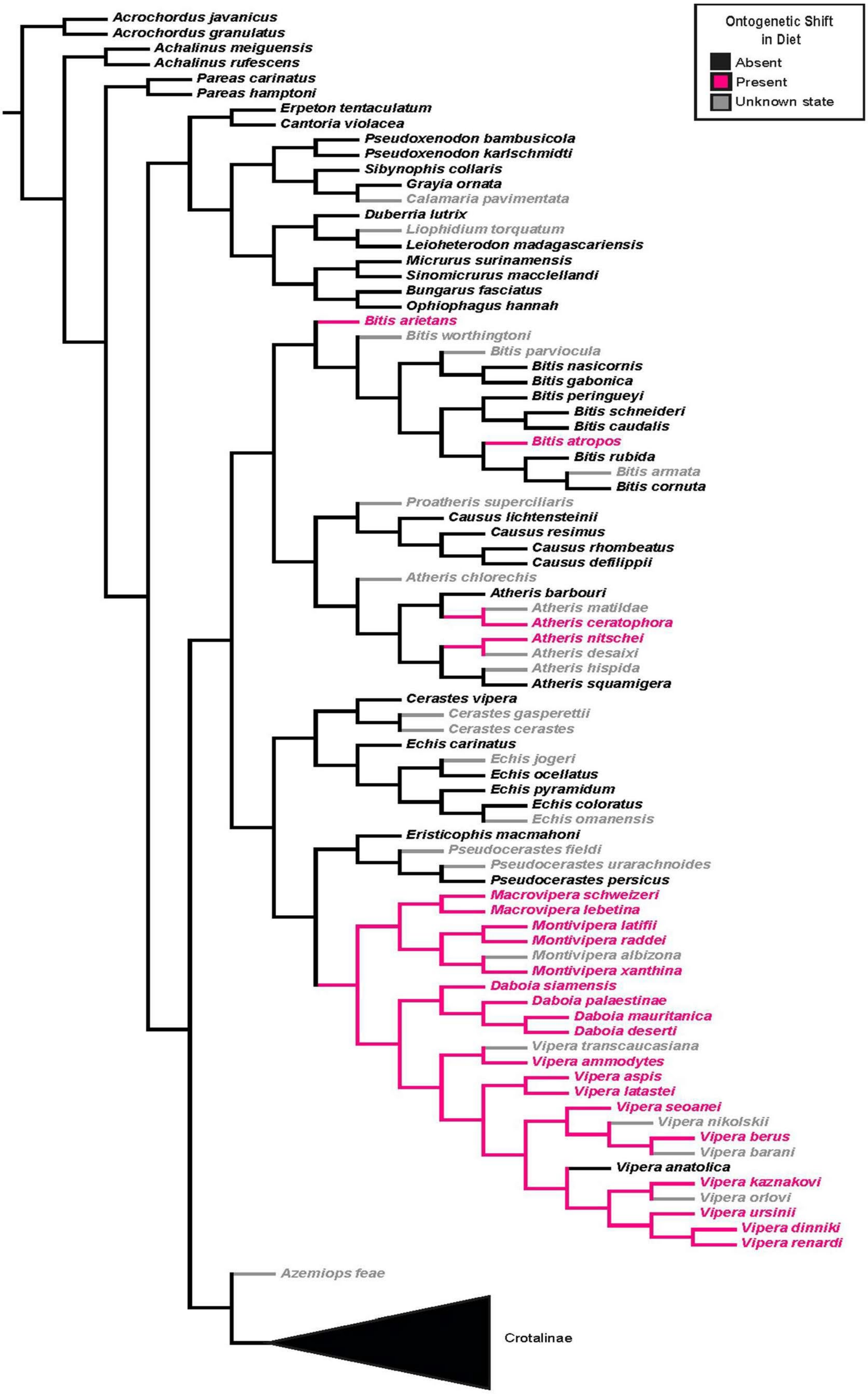


Figure 6. Parsimony ancestral state reconstruction for ontogenetic shifts in diet (OSD) made using ACCTRAN optimization (to be continued in the next page).

Figure 6 (continuation). Parsimony ancestral state reconstruction for ontogenetic shifts in diet (OSD) made using ACCTRAN optimization (to be continued in the next page).

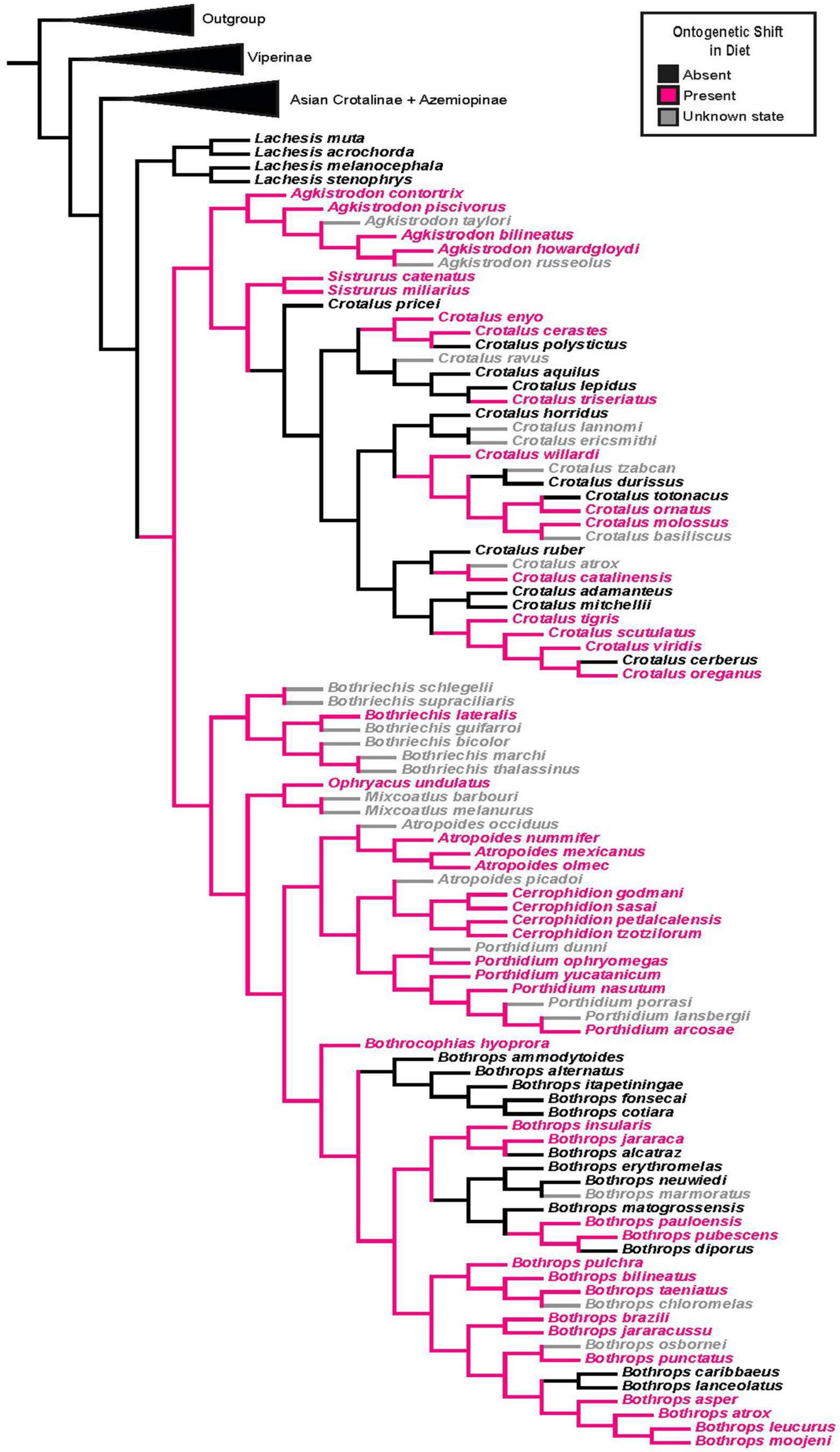


Figure 6 (continuation). Parsimony ancestral state reconstruction for ontogenetic shifts in diet (OSD) made using ACCTRAN optimization.

The pruned data matrix based only on species showing data on the ontogenetic shift in diet has 163 species (18 of which pertain to the outgroup). The ancestral state reconstruction of this dataset in the trimmed phylogenetic tree, made using maximum likelihood, is presented in Figure 5. The chosen model for state transition rates is the ARD model, which presented the lower Akaike value (LnL= -89.837, AICc= 185.825). The maximum likelihood reconstruction indicates that the ancestral of the Viperidae probably presented ontogenetic shift in diet from ectothermic to endothermic prey, differing from the parsimony results, (Fig. 5; Fig. S2, 99.8%), while all the species used as outgroup do not present such shift.

Several losses of this character occurred within the family, including the groups *Bitis* (except for *B. atropos* and *B. arietans), Causus*, *Lachesis*, and the *Bothrops alternatus* group. The ancestor of *Crotalus,* as well as the one of *Bothrops* presented ontogenetic shifts in diet (Fig. 5; Fig. S2, 100% and 99.8% of posterior probability, respectively), and most species of those genera kept the character along their evolution, while some species lost it afterwards (Fig. 5).

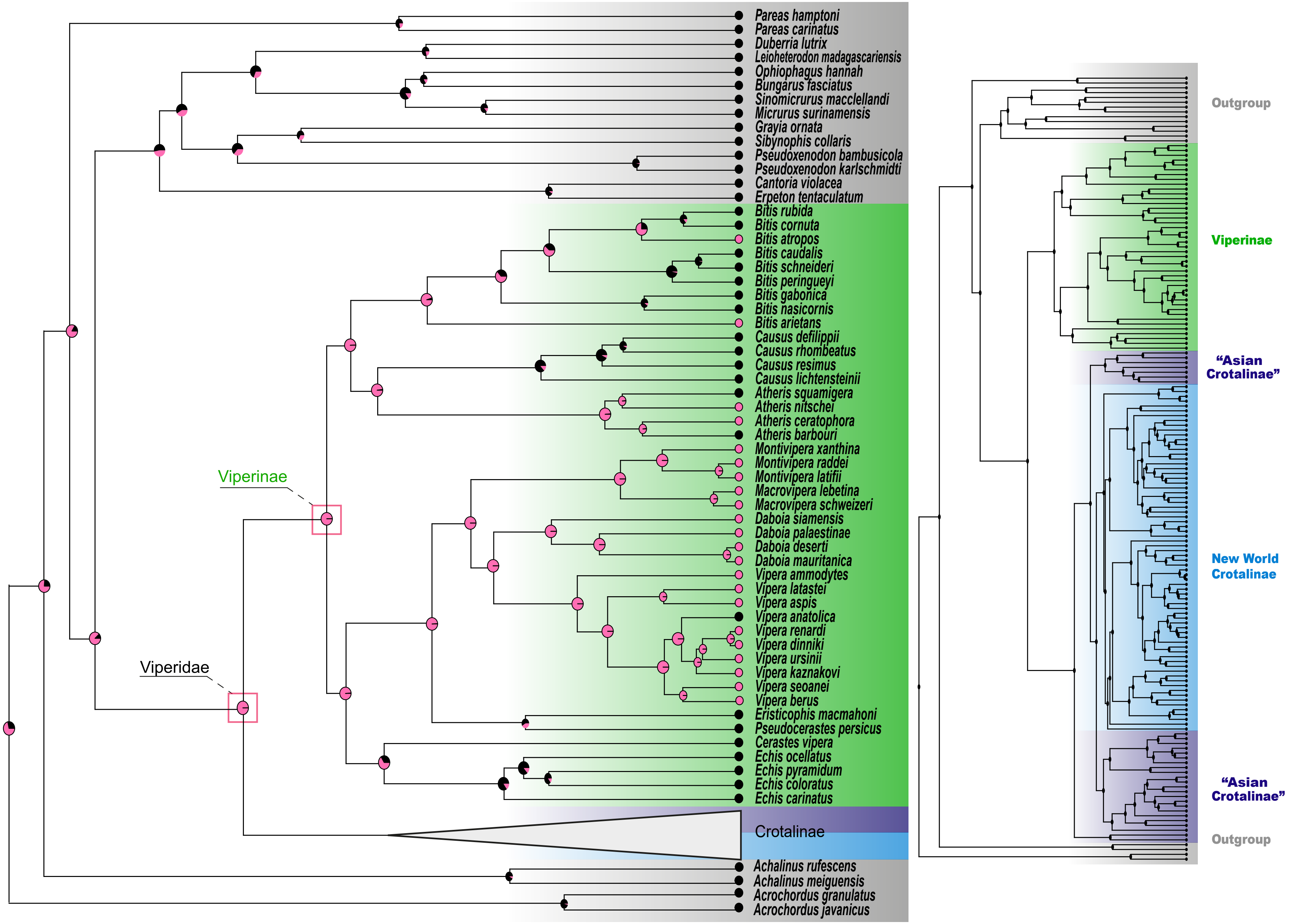


Figure 7. Ancestral state reconstruction using maximum likelihood for ontogenetic shifts in diet (OSD). The analysis was made using ARD model for state transition rates. Pie graphics at tree nodes are representing the proportional probabilities of the states. Pink: character present. Black: character absent (to be continued in next page).

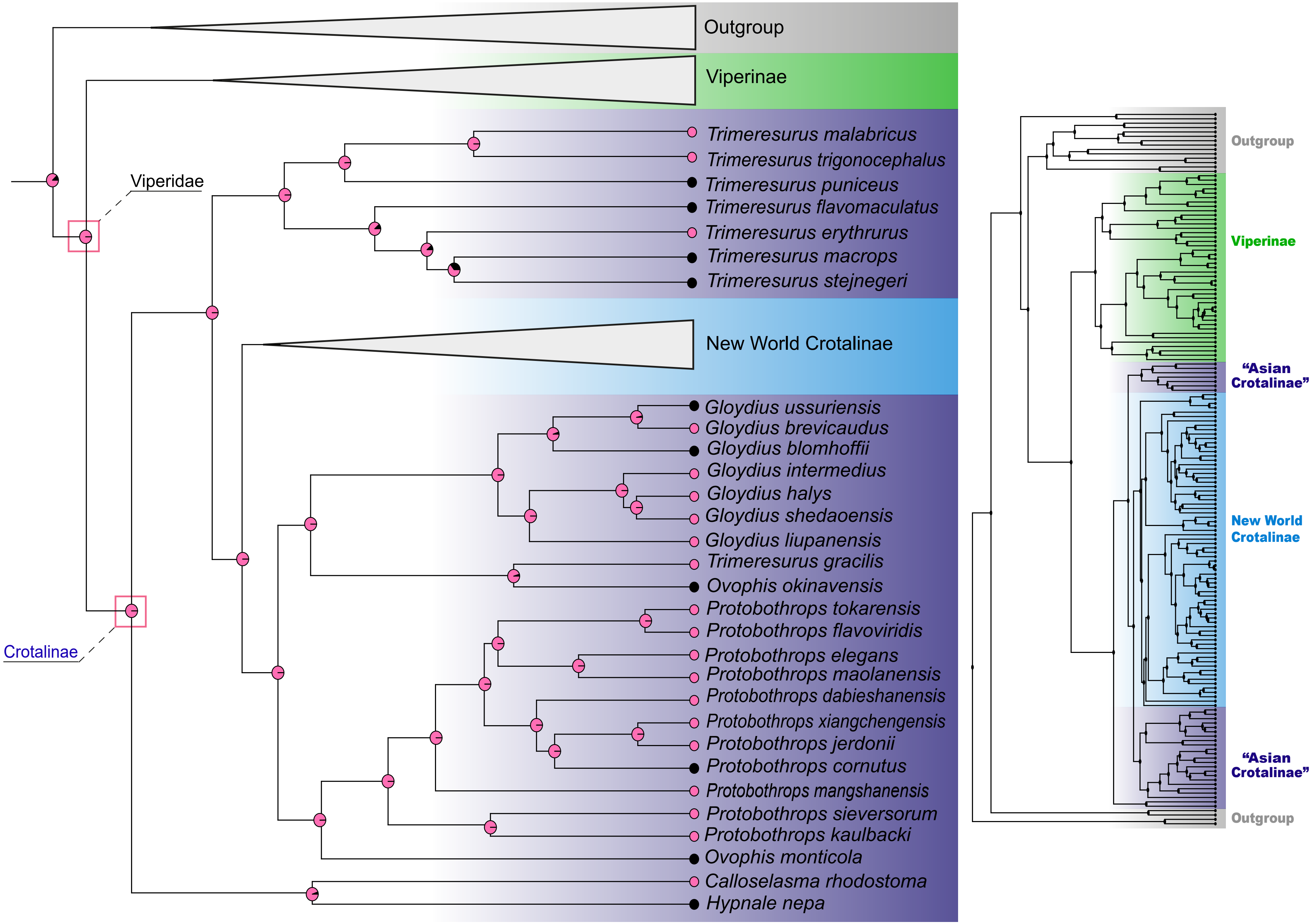


Figure 7 (continuation). Ancestral state reconstruction using maximum likelihood for ontogenetic shifts in diet (OSD). The analysis was made using ARD model for state transition rates. Pie graphics at tree nodes are representing the proportional probabilities of the states. Pink: character present. Black: character absent (to be continued in the next page).

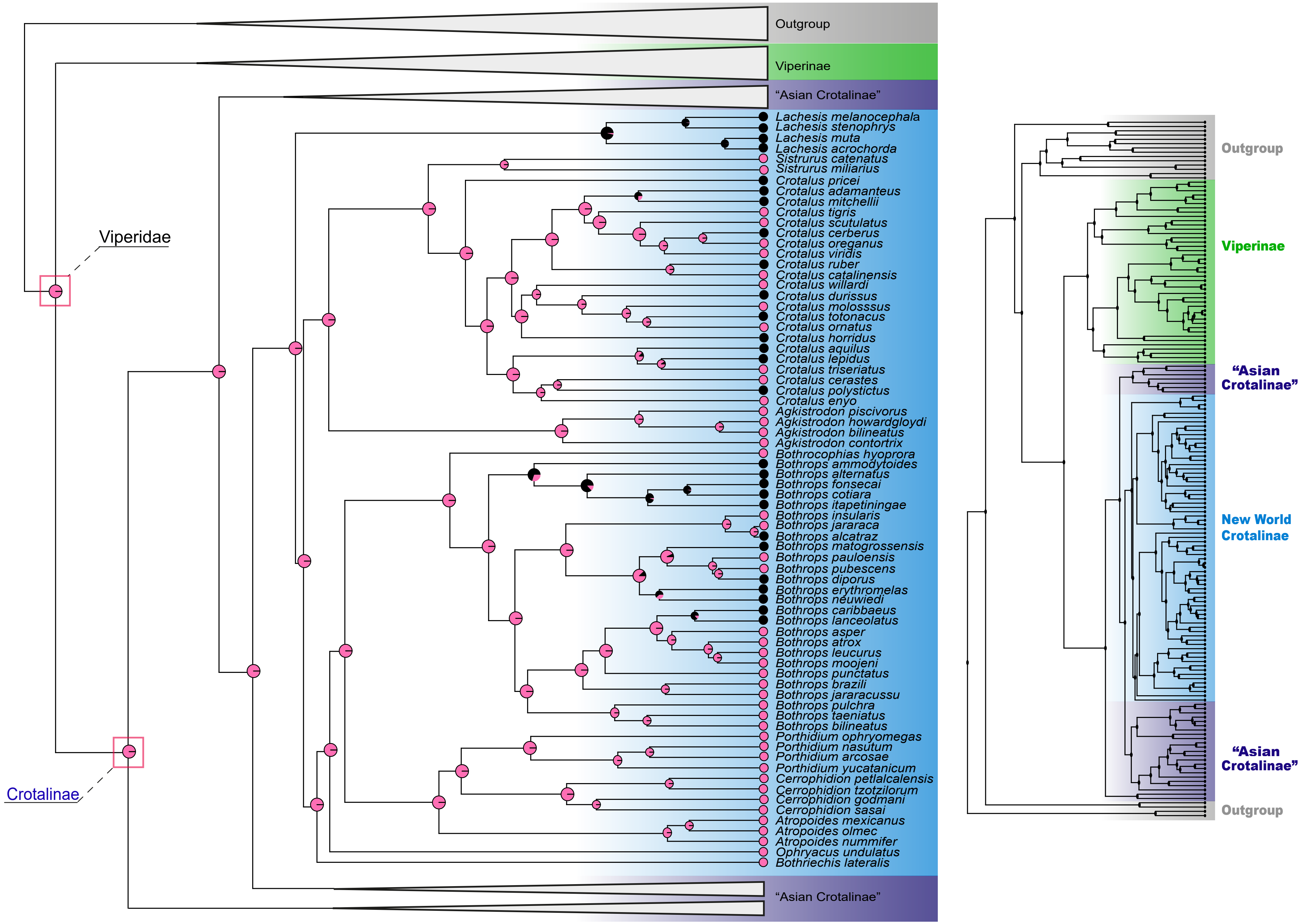


Figure 7 (continuation). Ancestral state reconstruction using maximum likelihood for ontogenetic shifts in diet (OSD). The analysis was made using ARD model for state transition rates. Pie graphics at tree nodes are representing the proportional probabilities of the states. Pink: character present. Black: character absent.

Phylogenetic Signal

All three analyzed characters showed strong phylogenetic signal, statistically different from zero (caudal luring $\lambda = 0.850$, $p = 0.001$; ontogenetic shift in diet $\lambda = 0.874$, $p = 0.002$; and conspicuous tail tips $\lambda = 0.874$, $p = 0.012$). The strong phylogenetic signal indicates that the states of those three characters are probably more correlated to the evolution of Viperidae groups than to ecological factors.

Correlation analyses between pairs of traits

Correlation between caudal luring and conspicuous tail tips

I tested the correlation between caudal luring and conspicuous tail tip (72 species with complete data, being 8 from the outgroup) under the ARD model of state transition (since caudal luring was not so well explained by the ER model, which was the best-fitted model for conspicuous tail tips). The test returned that the dependent model matrix explains the evolution of this pair of characters significantly better than the independent model, meaning that these characters evolved in a correlated fashion (Table 1, Figure 8).

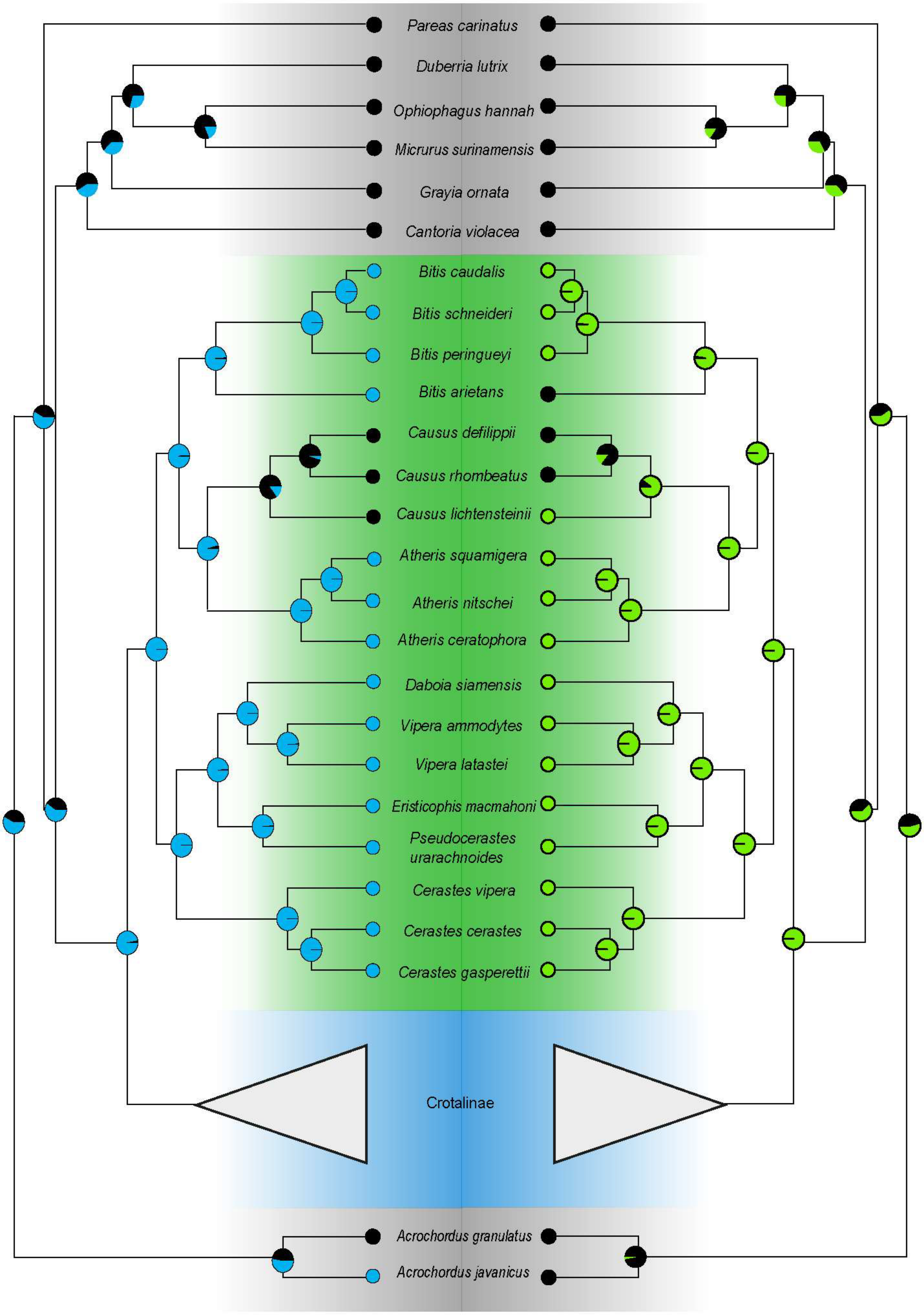


Figure 8. Mirrored trees with the ancestral state reconstruction for caudal luring (left) and conspicuous tail tips (right), under ARD model for state transition rates. Black: characters absent. Colors: characters present. Pie charts at tree nodes: posterior probabilities for each state (to be continued).

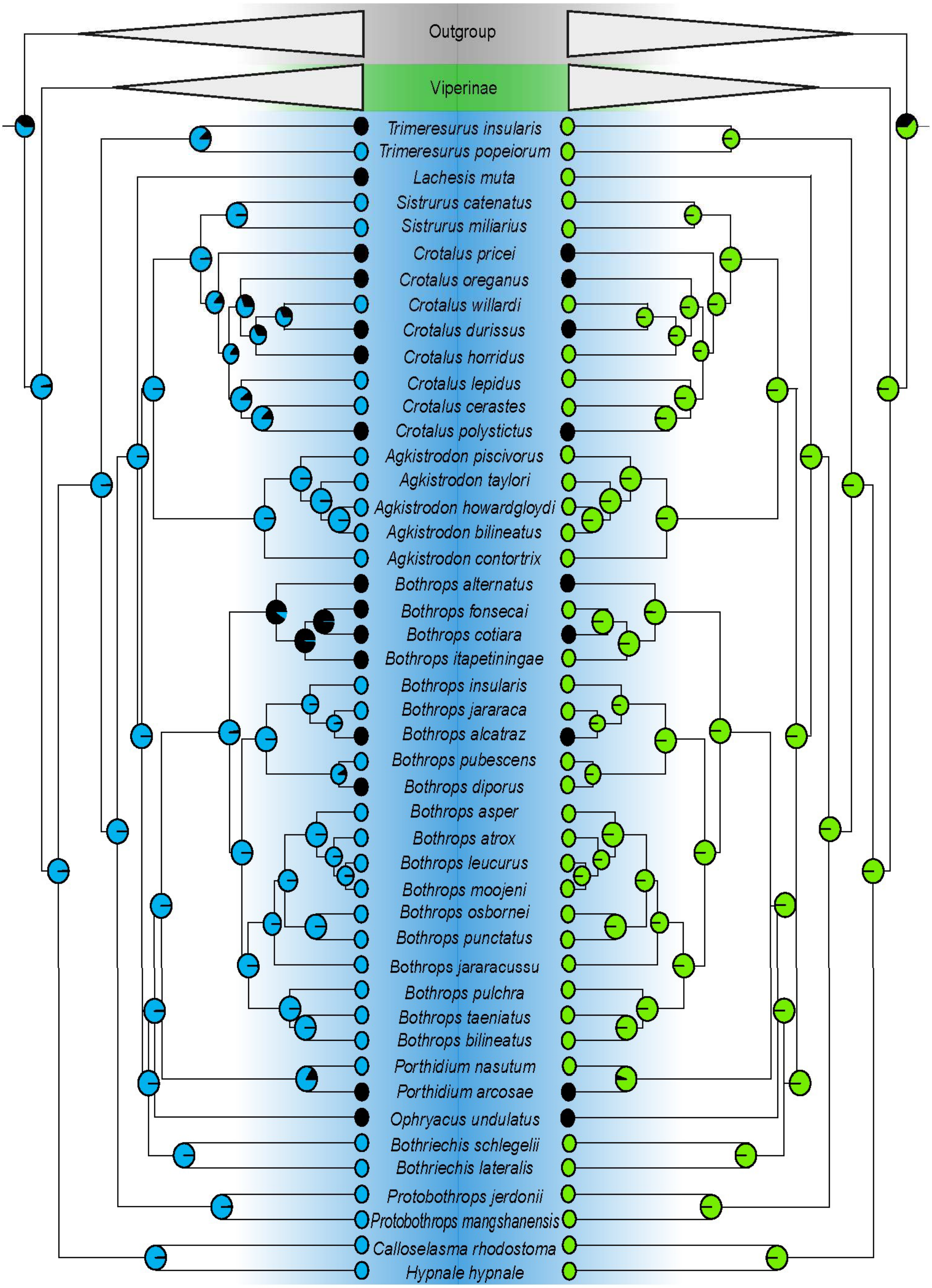


Figure 8 (continuation). Mirrored trees with the ancestral state reconstruction for caudal luring (left) and conspicuous tail tips (right), under ARD model for state transition rates. Black: characters absent. Colors: characters present. Pie charts at tree nodes: posterior probabilities for each state.

Correlation between caudal luring and ontogenetic shift in diet

For caudal luring and ontogenetic shift in diet (68 species with complete data, 10 from the outgroup), I tested their coevolution using the ARD model of state transition (best model fitted for both characters separately). My results indicate that the dependent model matrix is the best option to explain the evolution of these two characters (Figure 9, Table 1).

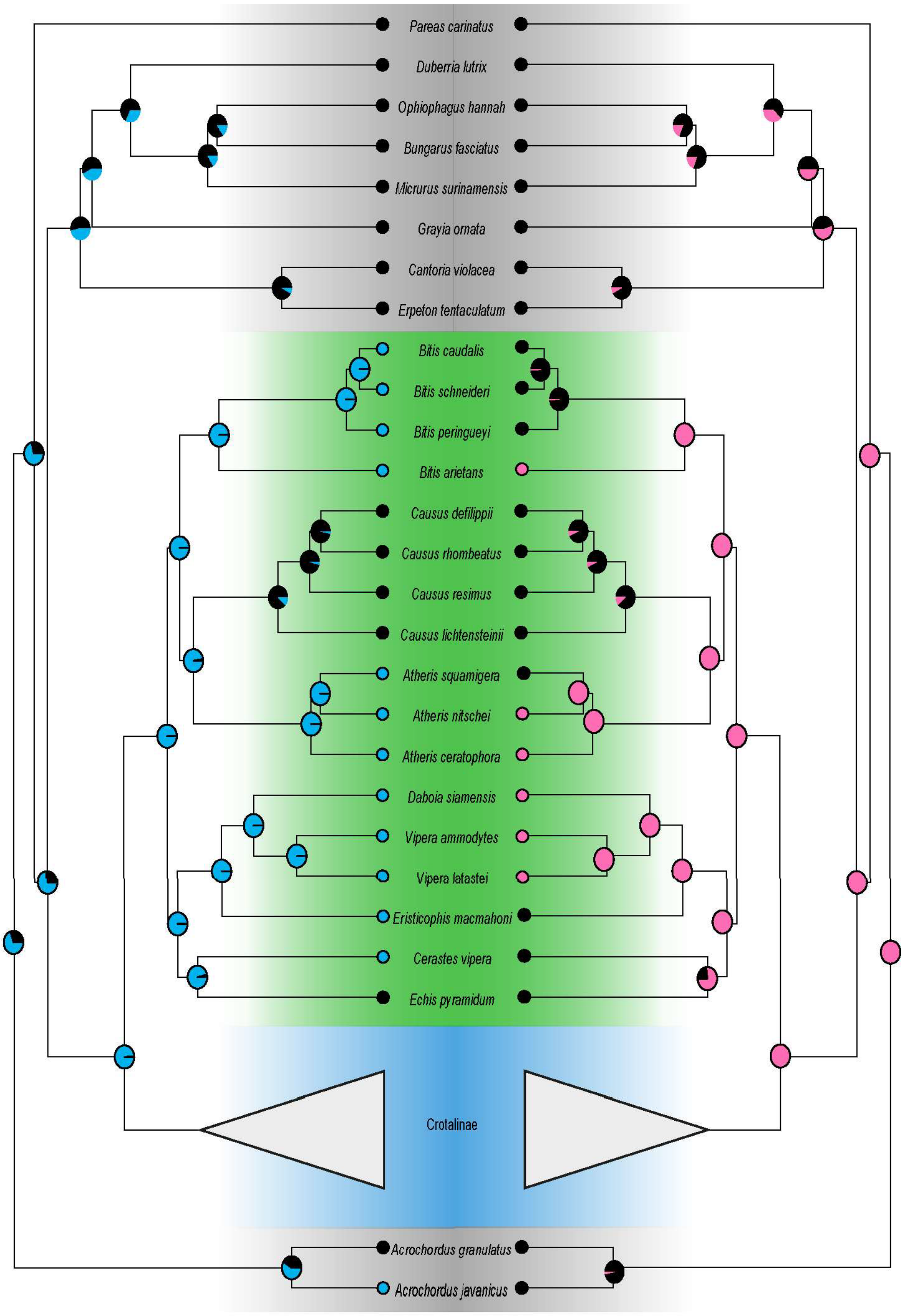


Figure 9. Mirrored trees with the ancestral state reconstruction for caudal luring (left) and ontogenetic shifts in diet (right) under the ARD model for state transition rates. Black: characters absent. Colors: characters present. Pie charts at tree nodes: posterior probabilities for each state (to be continued).

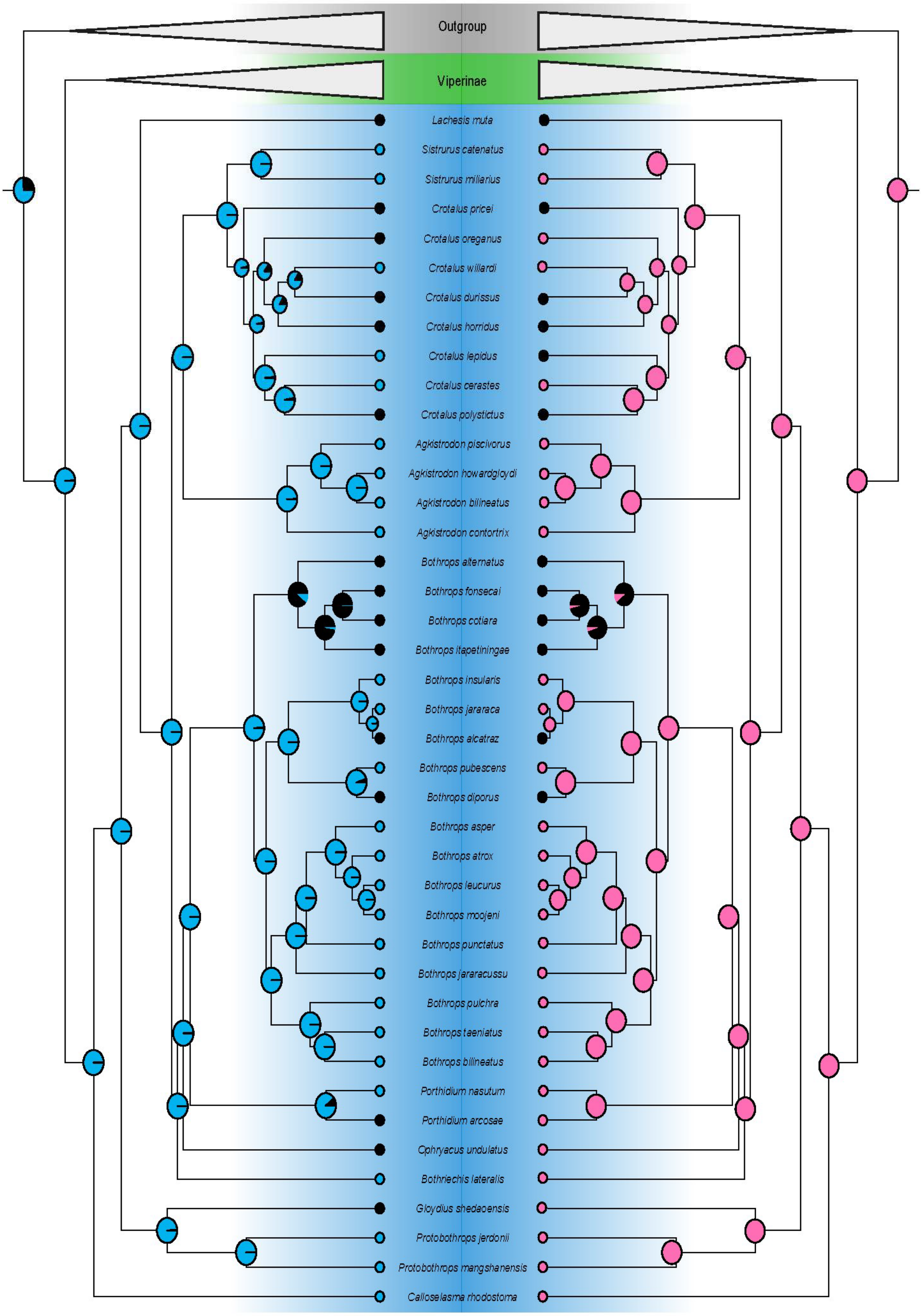


Figure 9 (continuation). Mirrored trees with the ancestral state reconstruction for caudal luring (left) and ontogenetic shifts in diet (right) under the ARD model for state transition rates. Black: characters absent. Colors: characters present. Pie charts at tree nodes: posterior probabilities for each state.

Correlation between conspicuous tail tips and ontogenetic shift in diet

Also using the ARD model (chosen with the same criteria as for the pair caudal luring-conspicuous tail tip), I tested the coevolution between conspicuous tail tips and ontogenetic shifts in diet (128 species, 10 outgroup), and found that the dependent model matrix had better scores than the opposite model (Figure 10, Table 1).

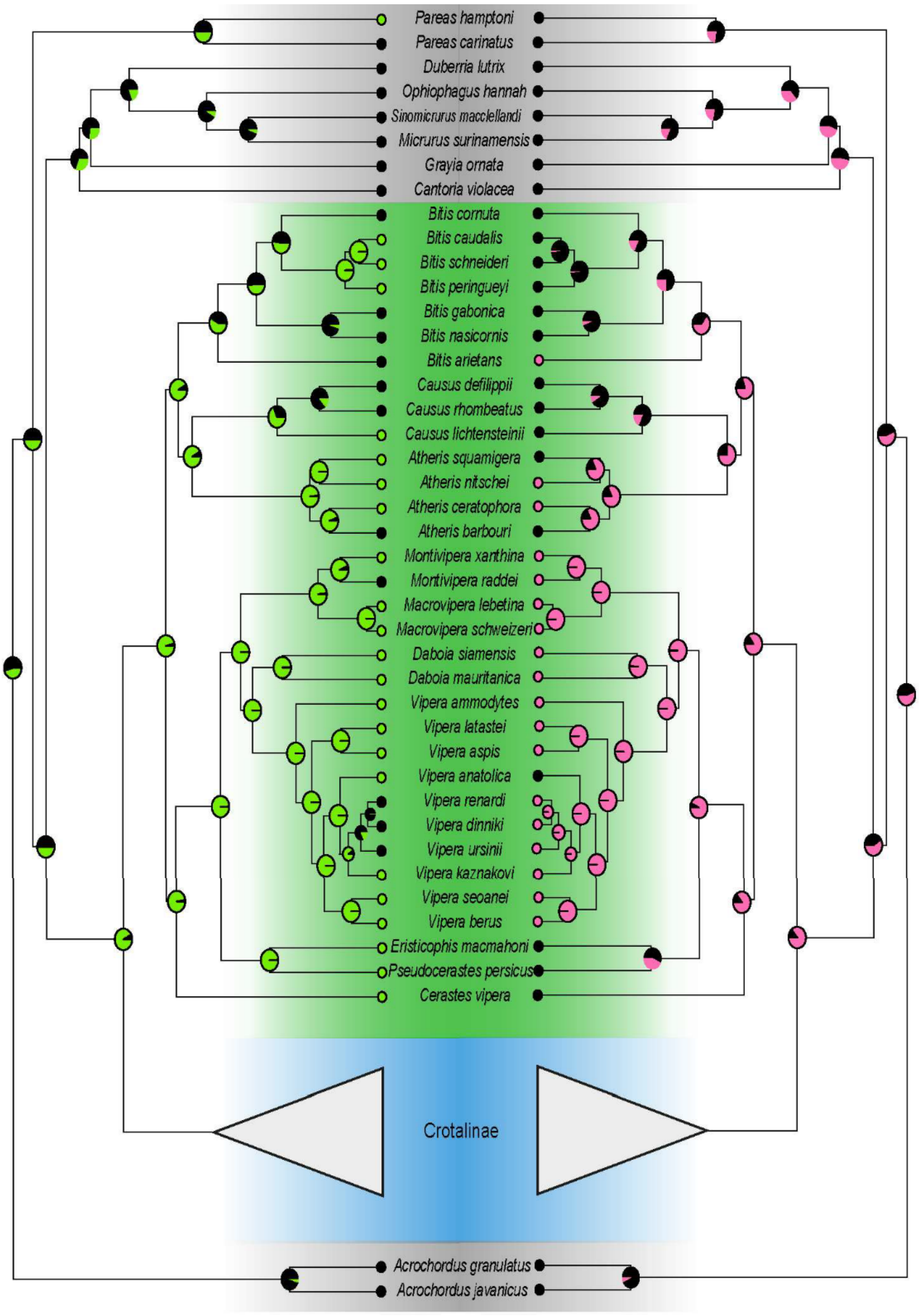


Figure 10. Mirrored trees with the ancestral state reconstruction for conspicuous tail tips (left) and ontogenetic shifts in diet (right) under the ARD model for state transition rates. Black: characters absent. Colors: characters present Pie charts at tree nodes: posterior probabilities for each state (to be continued).

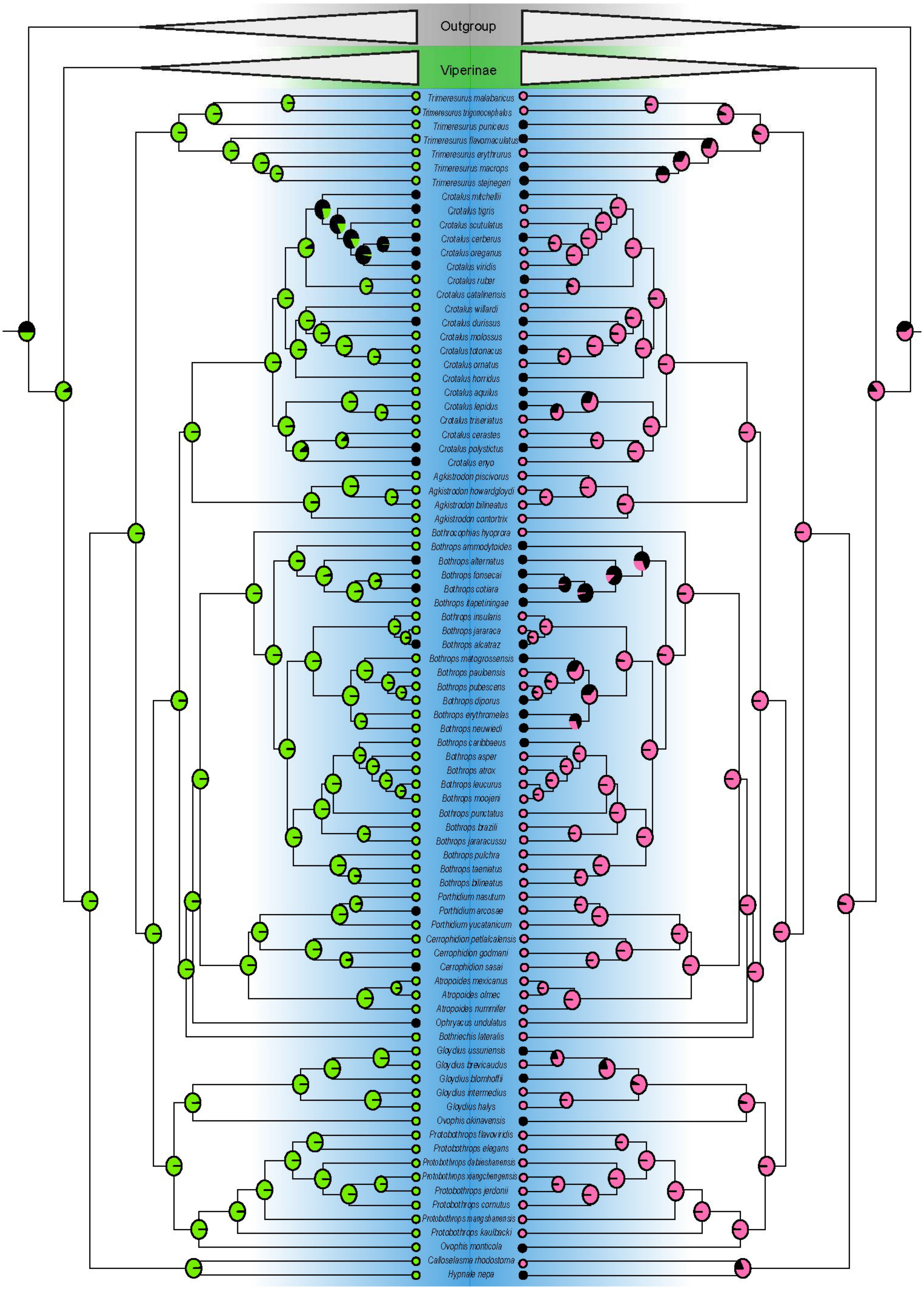
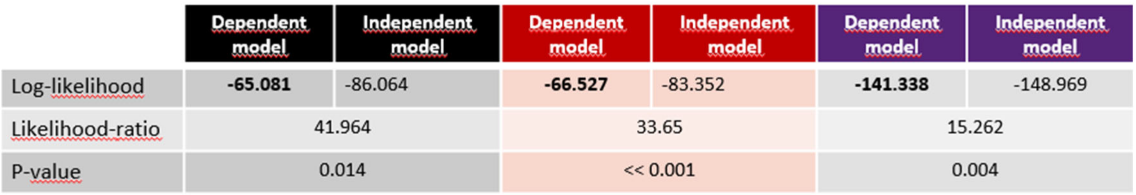


Figure 10 (continuation). Mirrored trees with the ancestral state reconstruction for conspicuous tail tips (left) and ontogenetic shifts in diet (right) under the ARD model for state transition rates. Black: characters absent. Colors: characters present. Pie charts at tree nodes: posterior probabilities for each state.

The dependent model rate matrix for each pair of traits has a significantly better log-likelihood score than the independent model rate matrix (Table 1), which suggests a correlated evolution between all pairs of characters.

Table 1. Scores of the dependent and independent rate matrix models of the correlation tests, for each pair of characters. Black: caudal luring and conspicuous tail tips. Red: caudal luring and ontogenetic shift in diet. Purple: conspicuous tail tips and ontogenetic shift in diet.



	Dependent model	Independent model	Dependent model	Independent model	Dependent model	Independent model
Log-likelihood	**-65.081**	-86.064	**-66.527**	-83.352	**-141.338**	-148.969
Likelihood-ratio	41.964		33.65		15.262	
P-value	0.014		<< 0.001		0.004	

DISCUSSION

Snakes are quite different from other vertebrates because of morphological, behavioral, and ecological constraints imposed by the lack of limbs (Greene, 1997; Lillywhite, 2014). Nevertheless, the group showed an astonishing diversity and the development of several foraging strategies, including specialized hunting tactics for prey approaching and capture (Vitt & Caldwell, 2014). One of the most striking of these strategies is the use of caudal luring, which is largely present in the Viperidae Family (Reiserer & Schuett, 2008). Herein, I suggest that the caudal luring is a characteristic that is strongly related to other natural history characteristics within the family, such as the presence of conspicuous tail tip and ontogenetic shift in the snakes' diet, from ectothermic to endothermic prey. These results reinforce the relevance of species' natural history characteristics for the understanding of Viperidae snakes’ evolution.

Based on my bibliographic revision, in which I found that most of the studied species had available information about the presence or absence of at least one of the three characters (CL, OSD, and CTT), there is still a great lack of information about the natural history of many species. The vast majority of studies involving viperids regard their venom and its pharmacological and epidemiological aspects. Among the characters investigated here, conspicuous tail tips returned the largest dataset. That is because, being a morphological character, information about its presence or absence could be taken in pictures from citizen science websites and other general sources, other than specific academic literature.

Herein, I conducted two series of comparative analyses based on the maximum parsimony paradigm and the maximum likelihood paradigm. Due to the particularities of such methods, I will explore a bit further the reasons why I chose to proceed with these analyses.

Parsimonious phylogenetic analyses are based on the assumption that the evolution of biological characteristics happened in the simplest way possible, with the minimal number of evolutionary changes (Fitch, 1971). Using Fitch's parsimony algorithm (1971) we can find out the number of character states transitions, as well as the ancestral character states in each node of the phylogenetic tree. However, parsimony methods have a different ontology than likelihood methods since they are not comparable and do not bring statistical information along with the data. Therefore, I also conducted maximum likelihood analyses to further explore the data.

As an alternative, one statistical method for phylogenetic analyses is the maximum likelihood approach. Likelihood is the "probability under a given model and parameter values that we would obtain the data that we actually see" (Harmon, 2019). Maximum likelihood methods are suited for comparative phylogenetic analyses because they take into consideration the data, the phylogeny, and an underlying model of evolution within a unique framework, to bring us the probability of the existence of such scenario (Pagel, 1997). Also, the likelihood approach returns only one most probable scenario, contrasting with parsimony, that might return more than one equally parsimonious reconstructions (Pagel, 1997).

In the context of comparative methods, the parsimony analyses are still important because they allow us to include taxa with missing information in the search for the most parsimonious scenario of character evolution. Furthermore, albeit the parsimony approach is not based on statistical models, Rindal and Brower (2011) showed that there is not enough difference between the results of the two approaches to justify the dismissal of parsimony when studying phylogenies.

All things considered, I gave a slight focus on the maximum likelihood analyses results because they are more detailed than the parsimony results, giving quantitative estimates of posterior probability and allowing the obtention of other estimates, like the objective trajectory of a trait evolution compared to another trait (Pagel, 1997).

Phylogenetic signal

I found that all analyzed characters present a strong phylogenetic signal. This shows that caudal luring, ontogenetic shift in diet, and conspicuous tail tips are conserved characters in the phylogeny, being present in the ancestor of the family (at least according to likelihood analyses) and evolving according to the species relations (phylogenetic dependence). Since the ancestral of Viperidae probably presented these characters, I hypothesized that environmental pressures were relevant for the emergence of these characters and their posterior maintenance along with the family diversification. However, the strong phylogenetic signal of OSD, CL, and CTT suggests that the maintenance of these characters on extant species is not necessarily related to selective pressures currently acting on those characters (Farrel, May & Andreadis*,* 2011).

The radiation of the vipers started in the Paleocene (around 64.5 Mya) with the diversification of the subfamilies Viperinae and Crotalinae happening during the Eocene (49.91 to 33.86 Mya) and from the middle of the Eocene to the late Oligocene (42.45 to 28.31 Mya), respectively (Alencar *et al.* 2016). The strong phylogenetic signal suggests that the presence or absence of the characters herein studied followed the family's phylogenetic branching process.

Accordingly, as showed in my results, most changes in character state happened in the common ancestors of large clades with one or more genera and were maintained along its evolution, with only a few punctual reversions. Thus, it indicates that the retention of ancestral states over time (phylogenetic conservatism) is a significant characteristic of caudal luring, ontogenetic shifts in diet, and conspicuous tail tip diversification in viperid snakes. This explains the fact that conspicuous tail tips are present in, virtually, all viperid groups, with only a few species in each group having lost this character.

Despite the strong phylogenetic signal found, secondary modifications on character states were found consistently in several terminal taxa. This could be related to other models of character evolution than the univariate Brownian model explaining the history of diversification in Viperidae. Such models would assume shifts in speciation rates, or differences in the phylogenetic signal strength along Viperidae evolution, for example. However, they were not tested herein due to limitations of the available analyses regarding discrete data.

Ancestral character state reconstructions

The most parsimonious scenario indicates that the ancestor of Viperidae had both caudal luring and conspicuous tail tips but lacked ontogenetic shifts in diet. On the other hand, the reconstruction based on maximum likelihood (ML) suggests the viperid ancestor presented all investigated characters, and that the three investigated features probably have an evolutionary correlation.

Those results indicate how the evolution of these characters probably happened, but it raises a few questions about what might have driven the evolution in a certain way. Regarding the most probable scenarios indicated by my data, I will discuss, further on, some hypotheses concerning the presented evolution of caudal luring, conspicuous tail tips, and ontogenetic shifts in diet in Viperidae.

Caudal luring

My results (for both parsimony and likelihood analyses) suggest that caudal luring evolved early in the phylogenetic history of Viperidae, being present on its ancestor. The Parsimony reconstruction suggests most of the viperid species should have caudal luring as one of its foraging strategies, despite the absence of information for 67.5% of species. Based on my review, likelihood reconstruction indicates a high probability (99.5%, Table S1) of caudal luring behavior in Viperidae ancestor.

Caudal luring evolution might be associated with anticipation or general neural excitation (Reiserer, 2002). It has been suggested that caudal luring happens in response to hunger and/or presence of prey, also that it misleads snakes' prey into attacking their tail (Greene & Campbell, 1972). Hagman *et al.* (2008) observations confirmed that caudal luring is induced by the approach of suitable prey and, also, it increases the number of opportunities to capture prey. This improvement in prey capture opportunities might lead to a positive selective pressure that maintained caudal luring in many Viperidae species along its evolutionary history. Considering the drastic climatic differences faced by Viperidae ancestors during Paleocene and Eocene (ancestor of Viperinae and Crotalinae lineages) we can suppose that this hunting strategy is effective to different prey taxa, such as anurans, lizards, and birds (e.g. Andrade *et al.,* 2010; del Marmol *et al.*, 2016)The homoplasic presence of this strategy in several snake families is putative evidence of caudal luring effectiveness for different prey types.

This selective advantage has been suggested to be correlated, as well, to coloration and movement sophistication that made the tail even more resembling to the prey item of the lured species, while visually dissociating the tail from the cryptic snake's body (Heatwole & Davison, 1976). That level of morphology and movement specialization can be explicitly seen in the tail of *Pseudocerastes urarachnoides* BOSTANCHI, ANDERSON, KAMI & PAPENFUSS, 2006 (Fig. 11). Thus, the efficacy of caudal luring might be correlated not only to the type of prey but also to the contrast between a conspicuous tail tip and a cryptic, camouflaged snake body, since there are available preys in the environment that would only respond when the snake is well camouflaged (Hagman *et al.* 2008). Finally, the context in which caudal luring is made is important since some prey would never respond to the luring while some are likely to react to the lure under various conditions (Hagman *et al.* 2008).

The presence of caudal luring has been inferred for *Bothrops* various times (Lira-da-Silva, 2009; Andrade *et al.* 2010; Carrasco, Leynaud & Scrocchi, 2010; Valencia, Garzón-Tello, Barragán-Paladines & Oxford, 2016), mainly because of the presence of a conspicuous tail tip in most *Bothrops* species. I found that 13 out of 29 (44.82%; 10 with missing information) species of the *Bothrops* genus present caudal luring, while almost all (86.2%) have conspicuous tail tips. According to my results on the parsimony analysis, even though the ancestor of *Bothrops* did not show caudal luring, the character evolved early in their lineage and should be present in most species, which corroborates the suggestions made throughout the literature (see above). More studies should be conducted on the natural history of these species for which caudal luring is inferred to confirm my results.

Only a few species of the *Trimeresurus* genus had available information about caudal luring as well as ontogenetic shifts in diet (two for CL and seven for OSD, of a total of 30 species), showing a significant lack of information regarding this group's natural history. Nevertheless, likelihood analyses indicate their ancestor presents both characters.

Rattlesnakes comprise both *Sistrurus* and *Crotalus* genera. All *Sistrurus* species present caudal luring, as well as ontogenetic shifts in diet and conspicuous tail tips. However, among the analyzed species, five *Crotalus* lost caudal luring, while three species maintained the character along the course of evolution. Likelihood analysis indicates the ancestor of *Crotalus* probably had caudal luring and it was lost subsequently in these five species.

On the other hand, my results suggest that the most parsimonious hypothesis shows the *Crotalus* ancestor without caudal luring, with the character resurfacing in the clade that includes both *C. cerates* and *C. lepidus*. Even without information about caudal luring in some rattlesnake species, this character is suggested for *C. enyo*, *C. ravus*, *C. aquilus*, and *C. triseriatus* in the parsimony analysis. Similar to species that do caudal lure (*C. lepidus*, *C. cerastes*, and *C. willardi*), these species are all relatively small, never exceeding 80cm in mean size. Similarities in their natural history might indicate cues for the presence of caudal luring in species in which it was never recorded, and further research directed to this subject might confirm the parsimony results presented in the current work.

Conspicuous tail tips

According to the results, conspicuous tail tips were originated early in Viperidae evolution, and it is present in most of its species, even in those that do not display caudal luring, such as *Lachesis muta, Crotalus horridus, Bothrops fonsecai, B. itapetiningae*, and *B. diporus*. This fact leads to a digression about conspicuous tail tips evolutionary origin. Although, I should emphasize that even though we can observe matches between form and function in characters (correlation), it is difficult to find strong evidence of empirical causation for those (Hagman *et al.* 2008).

Figure 11. Detail of the tail tip of *Pseudocerastes urarachnoides,* showing its remarkable resemblance to an arachnid.

The presence of a conspicuous tail tip seems essential to the display of caudal luring behavior, since its resemblance to worm-like invertebrates, along with tail movement, is what attracts the snake's prey (Heatwole & Davison, 1976; Reiserer & Schuett, 2008). Accordingly, I found that all viperid species showing caudal luring also have a conspicuous tail tip, except for *Bitis arietans*. However, lingual luring (attraction of prey by movements of the snake's tongue) is more effective in puff adders (*B. arietans*) than caudal luring in the attraction of prey (Glaudas & Alexander, 2016). This difference in effectiveness might be because of the contrasting coloration of the species tongue in comparison to the color of the head, while the snake had a uniform coloration on its tail and body (Glaudas & Alexander 2016).

It has been suggested that the pattern of cryptically colored snakes having different colored tail tips reflects a set of selective pressures for the presence of the conspicuous tail tips in snakes that display caudal luring (Farrel *et al.* 2011). However, there are no indications of current selections acting on conspicuous tail tips in *Sistrurus miliarius*, suggesting, instead, that the motion used in the luring might be more important to its effectiveness than its color (Farrel *et al.* 2011).

However, there is a possibility that even a small growth in foraging success due to conspicuous tail tips might lead to a positive selective pressure (Farrel *et al.* 2011). Since most caudal luring snakes lose their conspicuous tail following the first year of their life, any addition of prey in that initial year might be crucial to determine the individual's survival and, therefore, the selection of this (Farrel *et al.* 2011).

The loss of the conspicuous tail tip later in life was formerly suggested to be related to ontogenetic shifts in diet, in which the prey that is consumed in adulthood is not susceptible to luring (Heatwole & Davison, 1976). It is possible that, if the dietary shift is recent in this group's evolution, the conspicuous tail tip might remain as a vestigial character (Heatwole & Davison, 1976). Thus, this situation potentially explains cases I found in which conspicuous tail is present, but dietary shift and caudal luring are not (e.g. *Causus lichtensteinii, Crotalus horridus, Bothrops fonsecai, B. itapetiningae*, and *B. diporus*).

I found that the presence of a conspicuous tail tip does not always mean that species also present caudal luring, differently than what was previously suggested (Neill, 1960). Suitably, in this work, I found seven species that present a conspicuous tail tip but do not display caudal luring (*Causus lichtensteinii*, *Trimeresurus insularis*, *Lachesis muta*, *Crotalus horridus*, *Bothrops fonsecai*, *B. itapetiningae*, and *B. diporus*). At least three of these species' tail tips, although conspicuous, are not mimetic signals and, consequently, not eligible to caudal lure (*C. horridus, T. insularis*, and *L. muta*). The species *Causus lichtensteinii* is an active forager (Coimbra *et al.* 2018), which goes against the fundament of caudal luring, an ambush strategy. Also, all its congeners do not have conspicuous tail tips, indicating that this is a plesiomorphic character that was lost subsequently. Additionally, six of these species do not present ontogenetic shifts in diet, which is indicative of the importance of this character to the presence of caudal luring in a given species.

The absence of caudal luring does not mean that the conspicuous tail has no other function (Heatwole & Davison, 1976). There are several examples of tail display in snakes, and various possible explanations for it, other than the attraction of prey, including acting as a decoy, to divert attack to the tail, serving as a warning or intimidating signal, disorienting a predator with a "flash display", and it may have no recognized function at all (Greene, 1973).

The brightly colored tail is present in various species from different families, and it might be aposematic (warning the predator of the snake's venomous bite), which may lead to

Batesian mimicry from harmless species (Greene, 1973) and, also, it could intimidate the predator with a flash display, increasing the snake's time to flee while its predator is disoriented (Greene, 1973).

Many viperids display a conspicuous tail tip that does not resemble an invertebrate larva (Fig. 12), which might be correlated to the absence of caudal luring in some species (e. g. *Crotalus atrox, Crotalus ruber, Trimeresurus insularis*). The red color is frequent in aposematic displays. Species of the *Trimeresurus* genus often have a reddish coloration on their tail (see Sup. Material, Table S4: "Conspicuous Tail Tip"). Tail display has been observed in stress situations on *T. gramineus*, when individuals would thrash the tail from side to side, but tail movement was never seen in response to prey (Greene & Campbell, 1972). Such movements might relate to a flash or defensive display.

Rattlesnakes (*Crotalus*) form an important group with conspicuous tail tips. Out of 28 investigated species of rattlesnakes, there are 16 with conspicuous tail tips, while only three of those have records of caudal luring. Even though there are many rattlesnake species lacking information about natural history, assumptions can be made concerning the probability of the presence of caudal luring in rattlesnakes. The most recent species probably lack caudal luring while presenting conspicuous tail tips with more elaborate warning signals used as aposematic displays. Various rattlesnake species possess black and white bandings on their tail, which is thought to be aposematic signaling (Reiserer & Schuett, 2016). However, while those bright markings on the tail are not present in most basal species of rattlesnake, such as *C. pricei, C. aquilus, C. ravus*, and *C. polystictus*, the rattlesnake ancestor probably had caudal luring (posterior probability of 97.7%, Table S1), as does their sister genus, *Sistrurus* (Fig. 3). It has been suggested that caudal luring and mimicry had a key role in the evolution of the rattle, and that there was a transition from the larvae-like tail tip to warning signals that comprise elaborate aposematic displays, including black and white markings on the tail and loud rattling sounds (Reiserer & Schuett, 2016). Also, the type of prey consumed by the species must be taken into consideration, since two of the caudal luring species present ontogenetic shifts in diet, while the third eats mainly ectothermic prey in all stages of its life. Studies should be conducted regarding these species to confirm such assumptions.

Figure 12. Examples of conspicuous but not mimetic tail tips. A: *Crotalus ruber*, B: *Crotalus atrox*, C: *Trimeresurus insularis*, and D: *Crotalus horridus.*

Ontogenetic shift in diet

According to the ML results, ontogenetic shift in diet is an ancestral character for the family Viperidae. However, parsimony results did not conclude the same and returned ontogenetic shifts in diet with a scenario of at least 19 independents emergences along Viperidae evolution. It has been suggested that many differences between young and adult snakes regarding physiology, morphology, and behavior might lead to ontogenetic shifts in diet (Mushinsky, 1987, apud Andrade & Abe, 1999). The variety of prey that a snake can eat is limited by the gape of the mouth and, generally, the newborn snakes are too small to be able to swallow the same prey as the adults (Lillywhite, 2014; Girons, 1980). As the snake grows, the variety of prey types it can eat also increases (Girons, 1980). A study about the diet of nine species of European vipers (*Vipera ursinii, V. renardi, V. kaznakovi, V. seoanei, V. berus, V. aspis, V. latastei, V. monticola*, and *V. ammodytes*) (Girons, 1980), showed that the diet of the young changes progressively to become that of the adults when they reach around 40 cm. The author suggests that the ontogenetic shift in diet is related to competition avoidance between young and adult snakes since it was found that the biomass of viper populations is frequently greater than the biomass of their lizard prey. If the adult vipers would eat lizards at the same proportion as the juveniles, they would exert a severe predation pressure on lizard population, causing their depletion, which would reduce considerably the young vipers' chance of survival. Thus, there is a strong selective pressure toward ontogenetic shifts in diet (Girons, 1980). Further studies should be conducted to test if that hypothesis is valid on other viperids.

In my results, most of the species that present caudal luring also have ontogenetic shifts in diet (64.58%). However, some species that do not change the type of prey as they grow, such as *Bitis peringueyi*, *Bitis schneideri*, *Bitis caudalis*, and *Cerastes vipera* (Fig. 13), despite presenting caudal luring. Even though there is no ontogenetic shift in diet, these species continue to eat ectothermic prey as adults and, also, they are relatively small after reaching full size (Heatwole & Davison, 1976; Shine, Branch, Harlow & Webb, 1998; Reiserer & DeNardo, 2000; Maritz & Alexander, 2014). Therefore, the caudal luring might be present during the entire life of these species, targeting the same type of prey all along.

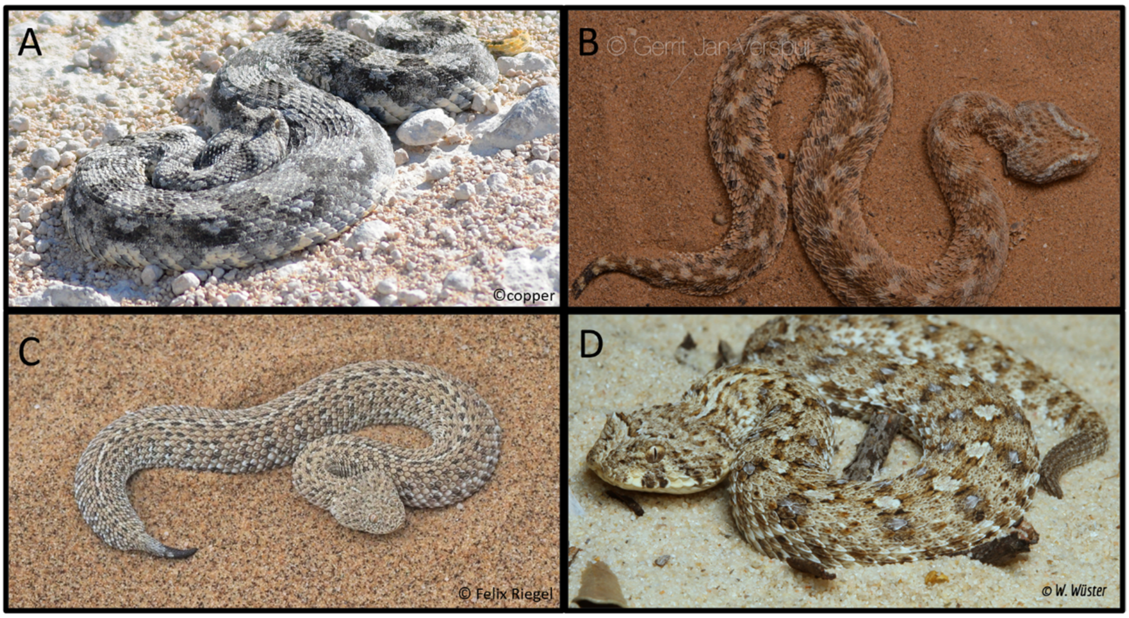


Figure 13. Species that have caudal luring but not ontogenetic shift in diet. A: *Bitis caudalis*, B: *Cerastes vipera*, C: *Bitis peringueyi* and D: *Bitis schneideri.*

CONCLUSIONS

The relationships between caudal luring and ontogenetic shift in diet, as well as caudal luring and conspicuous tail tips (especially those that mimic invertebrate larvae), has been suggested throughout scientific literature, but never tested up to this date.

In this study I gathered information about 220 viperid species (of 365 known so far), being the most comprehensive work on the evolution of caudal luring, ontogenetic shifts in diet from ectothermic to endothermic prey, and conspicuous tail tips, besides being the comparative work with the greatest number of species considered within a phylogenetic framework.

I found a correlation between all these three characters, as already suggested in the literature (*e.g.* Neill, 1960; Martins *et al.*, 2002; del Marmol *et al.*, 2016), but also found that their occurrence is more correlated to the shared evolution inside Viperidae than to current ecological constraints. Also, by studying individual species, or even small groups of closely related species, it has been proposed that caudal luring might be an ancestral character for the family Viperidae, along with conspicuous tail tips and ontogenetic shift in diet. Hence, I corroborate the ancestral condition of these characters in the evolution of viperid snakes using maximum likelihood methods, while parsimony optimized independent emergences for ontogenetic shifts in diet. My findings, however, were limited by the enormous gaps in natural history data on Viperid snakes, thus affecting some of my conclusions. Based on this, I suggest that more studies should bring further information on the natural history of viperid snakes, highlighting the relevance of basic studies on species ecology for the understanding of their evolution.

CONCLUSÕES

A relação entre engodo caudal e mudanças ontogenéticas na dieta, assim como entre engodo caudal e cauda conspícua (especialmente aquelas que mimetizam larvas de invertebrados), foi sugerida ao longo da literatura cientifica, porém jamais foi testada.

Neste trabalho eu coletei informações sobre 220 espécies de viperídeos (dentre as 365 conhecidas até o momento), resultando no mais completo trabalho sobre a evolução de engodo caudal, mudança ontogenética na dieta de presas ectotérmicas para presas endotérmicas, e cauda conspícua, além de ser o trabalho comparativo com maior número de espécies consideradas sob um contexto filogenético.

Encontrei uma correlação entre todos os três caracteres, como sugerido anteriormente na literatura (*e.g.* Neill, 1960; Martins *et al.*, 2002; del Marmol *et al.*, 2016), e, ainda, descobri que a sua ocorrência está mais correlacionada com a evolução compartilhada pelas espécies de Viperidae do que com restrições ecológicas. Além disso, a partir de estudos sobre espécies individuais, ou até pequenos grupos de espécies próximas, o engodo caudal foi proposto como um caráter ancestral da família Viperidae, juntamente com cauda conspícua e mudança ontogenética na dieta. Portanto, com este trabalho eu corroboro a condição ancestral destes caracteres na evolução de serpentes Viperidae através de análises de máxima verossimilhança, enquanto análises de parcimônia otimizam surgimentos independentes para mudança ontogenética na dieta.

Entretanto, meus resultados foram limitados por enormes lacunas em dados de história natural de viperídeos, o que pode ter afetado minhas conclusões. A partir disso, sugiro que futuros estudos tragam mais informações relacionadas à história natural de serpentes Viperidae, destacando a relevância de estudos de ciência básica sobre a ecologia das espécies para o entendimento da evolução das mesmas

BIBLIOGRAPHY

1. Alencar, L.R., Gaiarsa, M.P. & Martins, M. (2013) The evolution of diet and microhabitat use in pseudoboine snakes. *South American Journal of Herpetology,* **8,** 60-66.
2. Alencar, L.R., Quental, T.B., Grazziotin, F.G., Alfaro, M.L., Martins, M., Venzon, M. & Zaher, H. (2016) Diversification in vipers: Phylogenetic relationships, time of divergence and shifts in speciation rates. *Molecular Phylogenetics and Evolution,* **105,** 50-62.
3. Alencar, L.R.V., Martins, M., Burin, G. & Quental, T.B. (2017) Arboreality constrains morphological evolution but not species diversification in vipers. *Proceedings of the Royal Society B: Biological Sciences,* **284,** 20171775.
4. Andrade, D.V. & Abe, A.S. (1999) Relationship of venom ontogeny and diet in *Bothrops*. *Herpetologica***,** 200-204.
5. Andrade, D.V., Marques, O.A., Gavira, R.S., Barbo, F.E., Zacariotti, R.L. & Sazima, I. (2010) Tail luring by the golden lancehead (*Bothrops insularis*), an island endemic snake from south-eastern Brazil. *South American Journal of Herpetology,* **5,** 175-180.

6. Atkinson, E.C. (1997) Singing for your supper: acoustical luring of avian prey by northern shrikes. *The Condor,* **99,** 203-206.
7. Blomberg, S.P. & Garland Jr, T. (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology,* **15,** 899-910.
8. Carrasco, P., Scrocchi, G. & Leynaud, G. (2010) Redescription of the southernmost snake species, *Bothrops ammodytoides* (Serpentes: Viperidae: Crotalinae). *Amphibia-Reptilia,* **31,** 323-338.
9. Carvajal-Castro, J.D., López-Aguirre, Y., Ospina-L, A.M., Santos, J.C., Rojas, B. & Vargas-Salinas, F. (2020) Much more than a clasp: evolutionary patterns of amplexus diversity in anurans. *Biological Journal of the Linnean Society,* **129,** 652-663.
10. Chiszar, D., Boyer, D., Lee, R., Murphy, J.B. & Radcliffe, C.W. (1990) Caudal luring in the southern death adder, *Acanthophis antarcticus*. *Journal of Herpetology***,** 253-260.
11. de Pinna, M.C. (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics,* **7,** 367-394.
12. del Marmol, G.M., Mozaffari, O. & Gállego, J. (2016) *Pseudocerastes urarachnoides*: the ambush specialist. *Boletín de la Asociación Herpetológica Española,* **27,** 36-42.
13. Farrell, T.M., May, P.G. & Andreadis, P.T. (2011) Experimental Manipulation of Tail Color Does Not Affect Foraging Success in a Caudal Luring Rattlesnake. *Journal of Herpetology,* **45,** 291-293.
14. Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist,* **125,** 1-15.
15. Felsenstein, J. (2004) *Inferring phylogenies*. Sinauer Associates.
16. Fitch, W.M. (1971) Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Biology,* **20,** 406-416.
17. Girons, H.S. (1980) Modifications sélectives du régime des Vipères (Reptilia : Viperidae) lors de la croissance. *Amphibia-Reptilia,* **1,** 127-136.
18. Glaudas, X. & Alexander, G. (2016) A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake. *Behavioral Ecology and Sociobiology,* **71,** 1-7.

19. Greene, H.W. (1973) Defensive tail display by snakes and amphisbaenians. *Journal of Herpetology***,** 143-161.
20. Greene, H.W. & Campbell, J.A. (1972) Notes on the use of caudal lures by arboreal green pit vipers. *Herpetologica***,** 32-34.
21. Haddock, S., Moline, M. & Case, J. (2010) Bioluminescence in the sea. *Annual review of marine science,* **2,** 443-493.
22. Hagman, M., Phillips, B.L. & Shine, R. (2008) Tails of enticement: caudal luring by an ambush-foraging snake (*Acanthophis praelongus*, Elapidae). *Functional Ecology***,** 1134-1139.
23. Harmon, L.J. (2019) *Phylogenetic Comparative Methods: Learning from Trees*. EcoEvoRxiv.
24. Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics,* **24,** 129-131.
25. Harrel, J. & Stringer, G. (1997) Freeding Habits of the Alligator Snapping Turtle (*Macroclemys temminckii*) as Indicated by Teleosteam Otoliths. *Herpetological Review,* **28,** 185-187.
26. Heatwole, H. & Davison, E. (1976) A review of caudal luring in snakes with notes on its occurrence in the Saharan sand viper, *Cerastes vipera*. *Herpetologica***,** 332-336.
27. Jackson, R.R. (1992) Eight-legged tricksters. *Bioscience,* **42,** 590-598.
28. Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology,* **50,** 913-925.
29. Lillywhite, H.B. (2014) *How snakes work: structure, function and behavior of the world's snakes*. Oxford University Press.
30. Lira-da-Silva, R.M. (2009) *Bothrops leucurus* Wagler, 1824 (Serpentes; Viperidae): natural history, venom and envenomation. *Gazeta Médica da Bahia,* **79,** 56-65.
31. Mario-da-Rosa, C., Abegg, A.D., Malta-Borges, L., Righi, A.F., Bernarde, P.S., Cechin, S.Z. & dos Santos, T.G. (2020) A fisherman's tale: Activity, habitat use and the first evidence of lingual lure behavior in a South American snake. *SALAMANDRA,* **56,** 39-47.
32. Maritz, B. & Alexander, G.J. (2014) Namaqua Dwarf Adders are generalist predators. *African Journal of Herpetology,* **63,** 79-86.

33. Marques, O., Eterovic, A. & Sazima, I. (2019) *Serpentes da Mata Atlântica: Guia ilustrado para as florestas costeiras do Brasil*. Ponto A Editora, Cotia.
34. Marshall, D.C. & Hill, K.B. (2009) Versatile aggressive mimicry of cicadas by an Australian predatory katydid. *PLoS One,* **4,** e4185.
35. Martins, M., Marques, O.A. & Sazima, I. (2002) Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. *Biology of the Vipers***,** 307-328.
36. Menezes, J. & Santos, E. (2020) Habitat structure drives the evolution of aerial displays in birds. *The Journal of animal ecology,* **89,** 482-493.
37. Mullin, S.J. (1999) Caudal distraction by rat snakes (Colubridae, *Elaphe*): a novel behavior used when capturing mammalian prey. *The Great Basin Naturalist***,** 361-367.
38. Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K. & Thuiller, W. (2012) How to measure and test phylogenetic signal. *Methods in ecology and evolution,* **3,** 743-756.
39. Murphy, J.B., Carpenter, C.C. & Gillingham, J.C. (1978) Caudal luring in the green tree python, *Chondropython viridis* (Reptilia, Serpentes, Boidae). *Journal of Herpetology,* **12,** 117-119.
40. Nixon, K. (2002) WinClada, version 1.00. 08. *Published by the author, Ithaca, NY*, pp. 734-745.
41. Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **255,** 37-45.
42. Pagel, M. (1997) Inferring evolutionary processes from phylogenies. *Zoologica Scripta,* **26,** 331-348.
43. Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature,* **401,** 877-884.
44. Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics,* **20,** 289-290.
45. Paradis, E. & Schliep, K. (2018) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics,* **35,** 526-528.
46. R. Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

47. Radcliffe, C.W., Chiszar, D. & Smith, H. (1980) Prey-induced caudal movements in *Boa constrictor* with comments on the evolution of caudal luring. *Bulletin of the Maryland Herpetological Society,* **16,** 19-22.
48. Ramya, N., Kumar, P. V., Keerthi, M. C., Srinivasa, N., & Ramesh, K. B. (2017) Aggressive mimicry: A potential tool of Predators. *Journal of Pharmacognosy and Phytochemistry,* **6,** 1305-1307.
49. Reiserer, R. & Schuett, G. (2016) The origin and evolution of the rattlesnake rattle: misdirection, clarification, theory, and process. *Rattlesnakes of Arizona,* **2,** 247-274.
50. Reiserer, R.S. (2002) Stimulus control of caudal luring and other feeding responses: a program for research on visual perception in vipers. *Biology of the Vipers***,** 361-383.
51. Reiserer, R.S. & DeNardo, D.F. (2000) Natural history observations on *Bitis peringueyi* (Boulenger)(Reptilia: Viperidae). *Cimbebasia,* **16,** 195-198.
52. Reiserer, R.S. & Schuett, G.W. (2008) Aggressive mimicry in neonates of the sidewinder rattlesnake, *Crotalus cerastes* (Serpentes: Viperidae): stimulus control and visual perception of prey luring. *Biological Journal of the Linnean Society,* **95,** 81-91.
53. Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in ecology and evolution,* **3,** 217-223.
54. Rindal, E. & Brower, A.V.Z. (2011) Do model-based phylogenetic analyses perform better than parsimony? A test with empirical data. *Cladistics,* **27,** 331-334.
55. RStudio Team (2019) RStudio. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.
56. Sazima, I. & Puorto, G. (1993) Feeding technique of juvenile *Tropidodryas striaticeps*: probable caudal luring in a colubrid snake. *Copeia,* **1993,** 222-226.
57. Shine, R., Branch, W.R., Harlow, P.S. & Webb, J.K. (1998) Reproductive biology and food habits of horned adders, *Bitis caudalis* (Viperidae), from southern Africa. *Copeia,* **1998,** 391-401.
58. Uetz, P., Freed, P. & Hošek, J. (2020) The Reptile Database. Retrieved from *http://www.reptile-database.org*, accessed August, 2020.
59. Valencia, J.H., Garzón-Tello, K., Barragán-Paladines, M.E. & Oxford, P. (2016) *Serpientes venenosas del Ecuador: sistemática, taxonomía, historia natural,*

conservación, envenenamiento y aspectos antropológicos. Fundación Herpetológica Gustavo Orcés.

60. Vitt, L.J. & Caldwell, J.P. (2014) *Herpetology: an introductory biology of amphibians and reptiles,* 4th edn. Academic press.
61. Wignall, A.E. & Taylor, P.W. (2011) Assassin bug uses aggressive mimicry to lure spider prey. *Proceedings of the Royal Society B: Biological Sciences,* **278,** 1427-1433.

SUPLEMENTARY MATERIAL

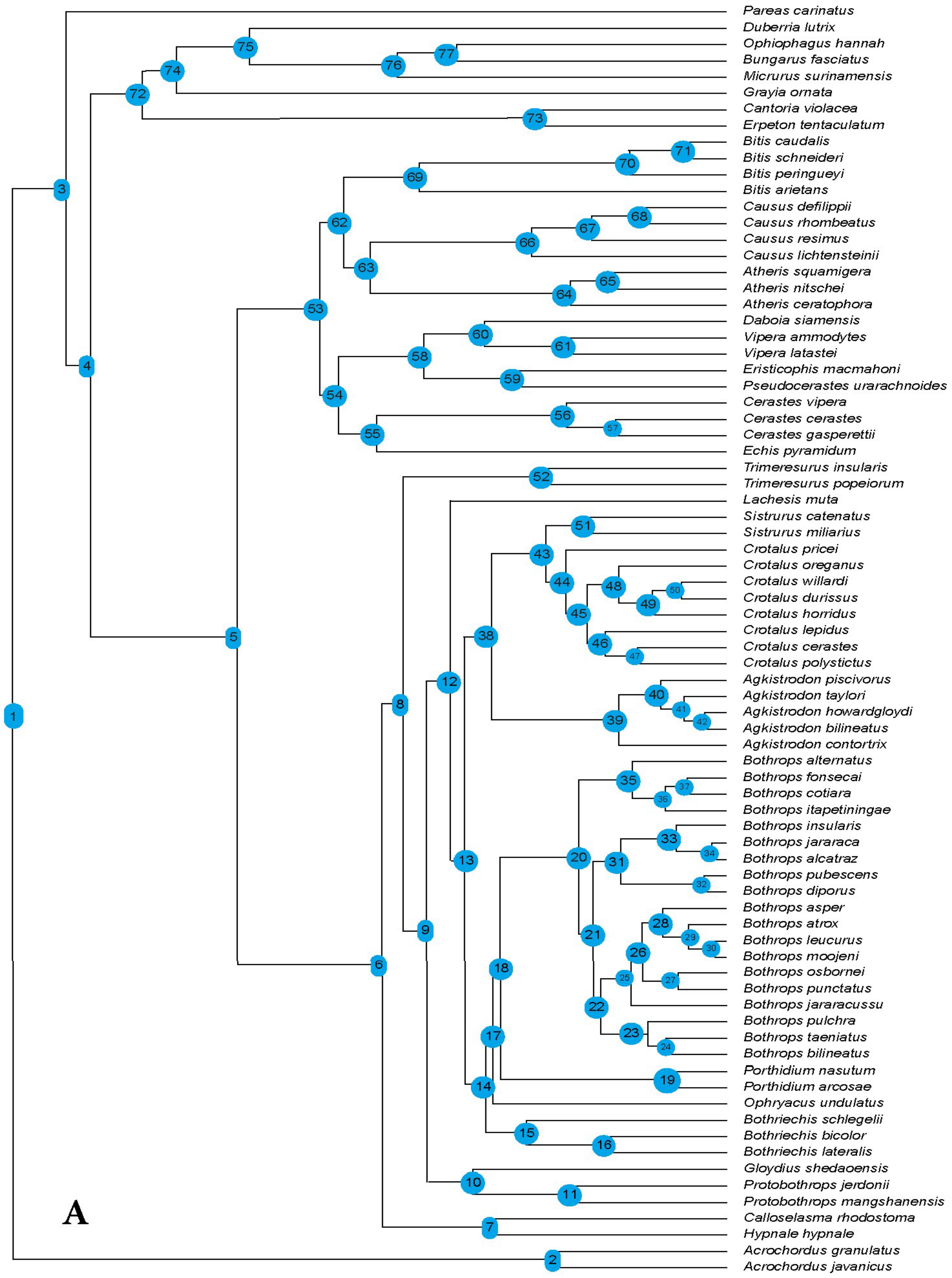


Figure S1. A: Phylogenetic tree with numbered nodes for caudal luring (CL), with posterior probability values of each state referred in Table S1.

Table S1. Table representing the values of probability of the caudal luring (CL) states for each node of the phylogeny in Figure S1.

	No	Yes		No	Yes		No	Yes		No	Yes		No	Yes		No	Yes
1	0.295	0.705	**14**	1.000	1.000	**27**	0.000	1.000	**40**	0.000	1.000	**53**	0.000	1.000	**66**	0.898	0.102
2	0.376	0.624	**15**	1.000	1.000	**28**	0.000	1.000	**41**	0.000	1.000	**54**	0.000	1.000	**67**	0.969	0.031
3	0.292	0.708	**16**	0.001	0.999	**29**	0.000	1.000	**42**	0.000	1.000	**55**	0.014	0.986	**68**	0.975	0.025
4	0.272	0.728	**17**	0.002	0.998	**30**	0.000	1.000	**43**	0.002	0.998	**56**	0.001	0.999	**69**	0.003	0.997
5	0.005	0.995	**18**	0.002	0.998	**31**	0.001	0.999	**44**	0.023	0.977	**57**	0.000	1.000	**70**	0.000	1.000
6	0.001	0.999	**19**	0.084	0.916	**32**	0.040	0.960	**45**	0.023	0.977	**58**	0.000	1.000	**71**	0.000	1.000
7	0.003	0.997	**20**	0.010	0.990	**33**	0.000	1.000	**46**	0.011	0.989	**59**	0.002	0.998	**72**	0.571	0.429
8	0.000	1.000	**21**	0.000	1.000	**34**	0.007	0.993	**47**	0.022	0.978	**60**	0.001	0.999	**73**	0.931	0.069
9	0.000	1.000	**22**	0.000	1.000	**35**	0.910	0.090	**48**	0.150	0.850	**61**	0.001	0.999	**74**	0.612	0.388
10	0.006	0.994	**23**	0.000	1.000	**36**	0.983	0.017	**49**	0.160	0.840	**62**	0.001	0.999	**75**	0.712	0.288
11	0.001	0.999	**24**	0.000	1.000	**37**	0.994	0.006	**50**	0.156	0.844	**63**	0.021	0.979	**76**	0.868	0.132
12	0.000	1.000	**25**	0.000	1.000	**38**	0.000	1.000	**51**	0.000	1.000	**64**	0.000	1.000	**77**	0.873	0.127
13	1.000	1.000	**26**	0.000	1.000	**39**	0.000	1.000	**52**	0.066	0.934	**65**	0.000	1.000			

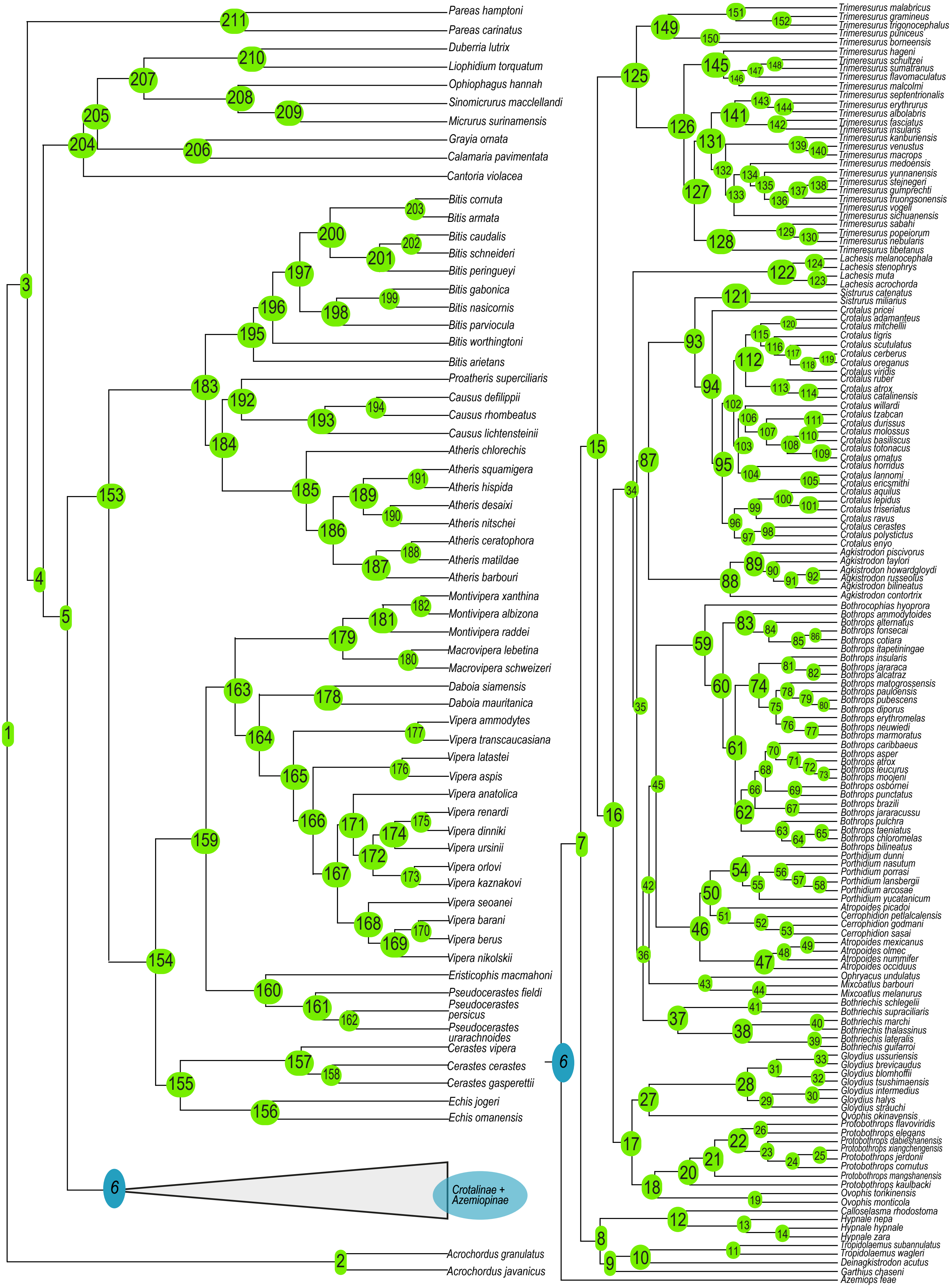


Figure S2. Phylogenetic tree with numbered nodes for conspicuous tail tips (CTT), with posterior probability values of each state referred in Table S2.

Table S2. Table representing the values of probability of the conspicuous tail tips (CTT) states for each node of the phylogeny in Figure S2.

	No	Yes		No	Yes		No	Yes		No	Yes		No	Yes		No	Yes
1	0.541	0.459	**37**	0.002	0.998	**73**	0.000	1.000	**109**	0.001	0.999	**145**	0.001	0.999	**181**	0.462	0.538
2	0.930	0.070	**38**	0.003	0.997	**74**	0.001	0.999	**110**	0.020	0.980	**146**	0.000	1.000	**182**	0.466	0.534
3	0.515	0.485	**39**	0.001	0.999	**75**	0.000	1.000	**111**	0.083	0.917	**147**	0.000	1.000	**183**	0.037	0.963
4	0.511	0.489	**40**	0.001	0.999	**76**	0.000	1.000	**112**	0.052	0.948	**148**	0.001	0.999	**184**	0.044	0.956
5	0.101	0.899	**41**	0.005	0.995	**77**	0.000	1.000	**113**	0.001	0.999	**149**	0.002	0.998	**185**	0.022	0.978
6	0.085	0.915	**42**	0.000	1.000	**78**	0.000	1.000	**114**	0.000	1.000	**150**	0.006	0.994	**186**	0.024	0.976
7	0.004	0.996	**43**	0.051	0.949	**79**	0.000	1.000	**115**	0.395	0.605	**151**	0.003	0.997	**187**	0.301	0.699
8	0.002	0.998	**44**	0.014	0.986	**80**	0.000	1.000	**116**	0.546	0.454	**152**	0.002	0.998	**188**	0.340	0.660
9	0.003	0.997	**45**	0.000	1.000	**81**	0.004	0.996	**117**	0.604	0.396	**153**	0.026	0.974	**189**	0.005	0.995
10	0.007	0.993	**46**	0.000	1.000	**82**	0.029	0.971	**118**	0.950	0.050	**154**	0.019	0.981	**190**	0.003	0.997
11	0.015	0.985	**47**	0.001	0.999	**83**	0.008	0.992	**119**	0.997	0.003	**155**	0.036	0.964	**191**	0.001	0.999
12	0.009	0.991	**48**	0.000	1.000	**84**	0.053	0.947	**120**	0.405	0.595	**156**	0.206	0.794	**192**	0.074	0.926
13	0.005	0.995	**49**	0.000	1.000	**85**	0.040	0.960	**121**	0.004	0.996	**157**	0.012	0.988	**193**	0.330	0.670
14	0.004	0.996	**50**	0.000	1.000	**86**	0.071	0.929	**122**	0.002	0.998	**158**	0.006	0.994	**194**	0.862	0.138
15	0.000	1.000	**51**	0.002	0.998	**87**	0.001	0.999	**123**	0.000	1.000	**159**	0.006	0.994	**195**	0.159	0.841
16	0.000	1.000	**52**	0.012	0.988	**88**	0.003	0.997	**124**	0.000	1.000	**160**	0.009	0.991	**196**	0.167	0.833
17	0.000	1.000	**53**	0.038	0.962	**89**	0.000	1.000	**125**	0.001	0.999	**161**	0.004	0.996	**197**	0.226	0.774
18	0.001	0.999	**54**	0.001	0.999	**90**	0.000	1.000	**126**	0.000	1.000	**162**	0.002	0.998	**198**	0.326	0.674
19	0.006	0.994	**55**	0.000	1.000	**91**	0.000	1.000	**127**	0.001	0.999	**163**	0.006	0.994	**199**	0.903	0.097
20	0.001	0.999	**56**	0.000	1.000	**92**	0.000	1.000	**128**	0.033	0.967	**164**	0.004	0.996	**200**	0.249	0.751
21	0.001	0.999	**57**	0.002	0.998	**93**	0.002	0.998	**129**	0.001	0.999	**165**	0.002	0.998	**201**	0.007	0.993
22	0.000	1.000	**58**	0.012	0.988	**94**	0.008	0.992	**130**	0.000	1.000	**166**	0.001	0.999	**202**	0.001	0.999
23	0.000	1.000	**59**	0.001	0.999	**95**	0.006	0.994	**131**	0.000	1.000	**167**	0.001	0.999	**203**	0.996	0.004
24	0.000	1.000	**60**	0.000	1.000	**96**	0.011	0.989	**132**	0.001	0.999	**168**	0.000	1.000	**204**	0.664	0.336
25	0.000	1.000	**61**	0.000	1.000	**97**	0.126	0.874	**133**	0.001	0.999	**169**	0.000	1.000	**205**	0.701	0.299
26	0.001	0.999	**62**	0.000	1.000	**98**	0.136	0.864	**134**	0.000	1.000	**170**	0.000	1.000	**206**	0.780	0.220
27	0.003	0.997	**63**	0.000	1.000	**99**	0.003	0.997	**135**	0.000	1.000	**171**	0.007	0.993	**207**	0.746	0.254
28	0.008	0.992	**64**	0.000	1.000	**100**	0.000	1.000	**136**	0.004	0.996	**172**	0.066	0.934	**208**	0.884	0.116
29	0.027	0.973	**65**	0.000	1.000	**101**	0.000	1.000	**137**	0.001	0.999	**173**	0.003	0.997	**209**	0.920	0.080
30	0.002	0.998	**66**	0.000	1.000	**102**	0.006	0.994	**138**	0.000	1.000	**174**	0.808	0.192	**210**	0.641	0.359
31	0.001	0.999	**67**	0.001	0.999	**103**	0.006	0.994	**139**	0.053	0.947	**175**	0.999	0.001	**211**	0.505	0.495
32	0.000	1.000	**68**	0.000	1.000	**104**	0.030	0.970	**140**	0.006	0.994	**176**	0.001	0.999			
33	0.000	1.000	**69**	0.000	1.000	**105**	0.948	0.052	**141**	0.004	0.996	**177**	0.001	0.999			
34	0.000	1.000	**70**	0.000	1.000	**106**	0.004	0.996	**142**	0.074	0.926	**178**	0.010	0.990			
35	0.000	1.000	**71**	0.000	1.000	**107**	0.005	0.995	**143**	0.001	0.999	**179**	0.166	0.834			
36	0.000	1.000	**72**	0.000	1.000	**108**	0.003	0.997	**144**	0.000	1.000	**180**	0.002	0.998			

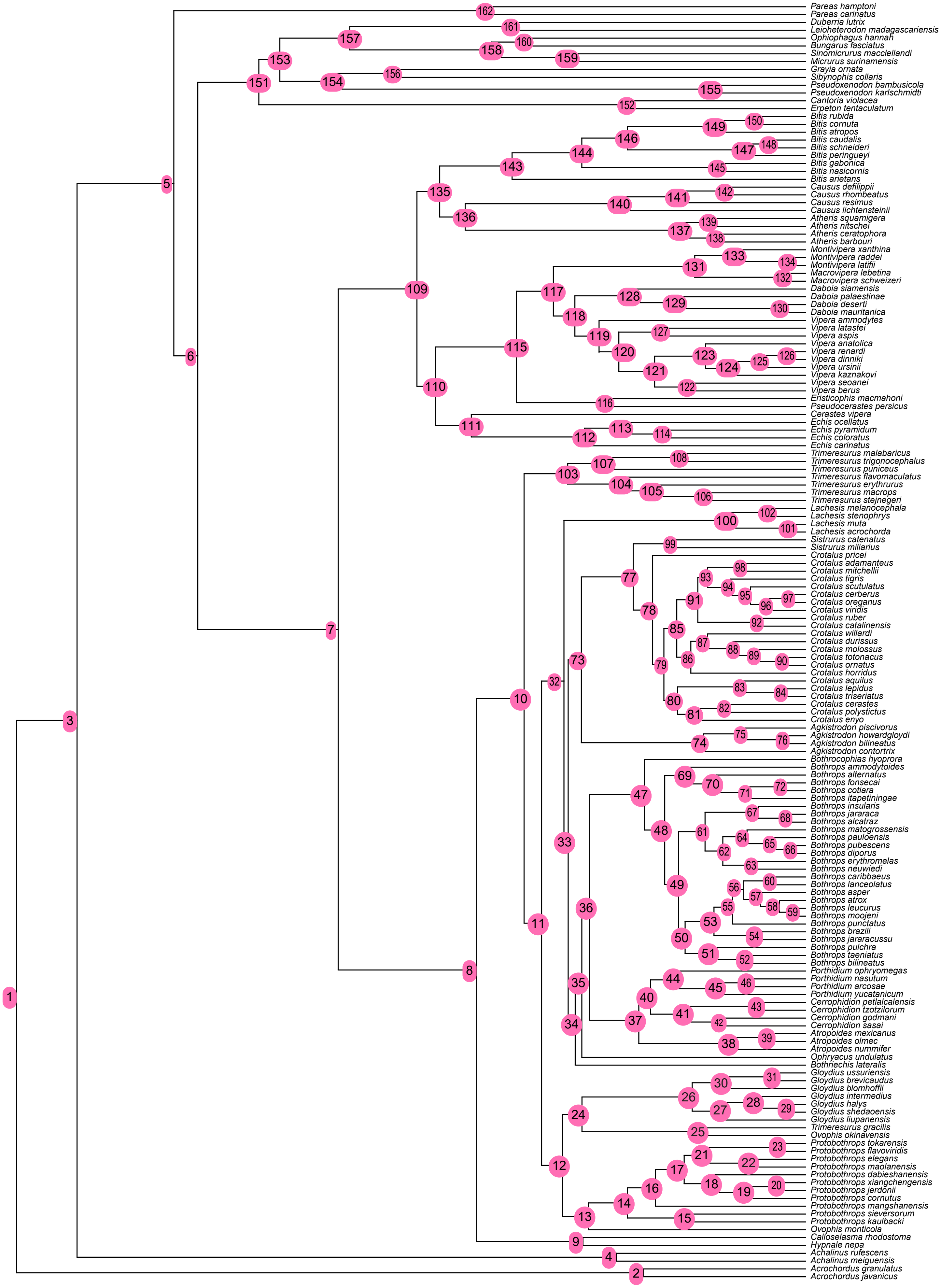


Figure S3. Phylogenetic tree with numbered nodes for ontogenetic shift in diet (OSD), with posterior probability values of each state referred in Table S3.

Table S3. Table representing the values of probability of the ontogenetic shift in diet (OSD) states for each node of the phylogeny in Figure S3.

	No	Yes		No	Yes		No	Yes		No	Yes		No	Yes		No	Yes
1	0.285	0.715	**28**	0.000	1.000	**55**	0.000	1.000	**82**	0.003	0.997	**109**	0.004	0.996	**136**	0.022	0.978
2	0.965	0.035	**29**	0.000	1.000	**56**	0.003	0.997	**83**	0.110	0.890	**110**	0.012	0.988	**137**	0.014	0.986
3	0.239	0.761	**30**	0.052	0.948	**57**	0.000	1.000	**84**	0.085	0.915	**111**	0.341	0.659	**138**	0.019	0.981
4	0.930	0.070	**31**	0.035	0.965	**58**	0.000	1.000	**85**	0.000	1.000	**112**	0.852	0.148	**139**	0.015	0.985
5	0.163	0.837	**32**	0.000	1.000	**59**	0.000	1.000	**86**	0.000	1.000	**113**	0.866	0.134	**140**	0.870	0.130
6	0.120	0.880	**33**	0.000	1.000	**60**	0.868	0.132	**87**	0.000	1.000	**114**	0.875	0.125	**141**	0.930	0.070
7	0.002	0.998	**34**	0.000	1.000	**61**	0.002	0.998	**88**	0.002	0.998	**115**	0.008	0.992	**142**	0.937	0.063
8	0.001	0.999	**35**	0.000	1.000	**62**	0.117	0.883	**89**	0.000	1.000	**116**	0.587	0.413	**143**	0.049	0.951
9	0.055	0.945	**36**	0.000	1.000	**63**	0.621	0.379	**90**	0.003	0.997	**117**	0.000	1.000	**144**	0.364	0.636
10	0.000	1.000	**37**	0.000	1.000	**64**	0.068	0.932	**91**	0.000	1.000	**118**	0.000	1.000	**145**	0.907	0.093
11	0.000	1.000	**38**	0.000	1.000	**65**	0.001	0.999	**92**	0.019	0.981	**119**	0.000	1.000	**146**	0.382	0.618
12	0.000	1.000	**39**	0.000	1.000	**66**	0.001	0.999	**93**	0.001	0.999	**120**	0.000	1.000	**147**	0.969	0.031
13	0.002	0.998	**40**	0.000	1.000	**67**	0.000	1.000	**94**	0.000	1.000	**121**	0.000	1.000	**148**	0.982	0.018
14	0.000	1.000	**41**	0.000	1.000	**68**	0.004	0.996	**95**	0.000	1.000	**122**	0.000	1.000	**149**	0.248	0.752
15	0.000	1.000	**42**	0.000	1.000	**69**	0.703	0.297	**96**	0.000	1.000	**123**	0.001	0.999	**150**	0.867	0.133
16	0.000	1.000	**43**	0.000	1.000	**70**	0.869	0.131	**97**	0.006	0.994	**124**	0.000	1.000	**151**	0.531	0.469
17	0.000	1.000	**44**	0.000	1.000	**71**	0.952	0.048	**98**	0.745	0.255	**125**	0.000	1.000	**152**	0.922	0.078
18	0.000	1.000	**45**	0.000	1.000	**72**	0.972	0.028	**99**	0.000	1.000	**126**	0.000	1.000	**153**	0.590	0.410
19	0.000	1.000	**46**	0.000	1.000	**73**	0.000	1.000	**100**	0.965	0.035	**127**	0.000	1.000	**154**	0.640	0.360
20	0.000	1.000	**47**	0.000	1.000	**74**	0.000	1.000	**101**	0.996	0.004	**128**	0.000	1.000	**155**	0.972	0.028
21	0.000	1.000	**48**	0.002	0.998	**75**	0.000	1.000	**102**	0.984	0.016	**129**	0.000	1.000	**156**	0.670	0.330
22	0.000	1.000	**49**	0.000	1.000	**76**	0.000	1.000	**103**	0.007	0.993	**130**	0.000	1.000	**157**	0.692	0.308
23	0.000	1.000	**50**	0.000	1.000	**77**	0.000	1.000	**104**	0.118	0.882	**131**	0.000	1.000	**158**	0.850	0.150
24	0.000	1.000	**51**	0.000	1.000	**78**	0.000	1.000	**105**	0.116	0.884	**132**	0.000	1.000	**159**	0.867	0.133
25	0.045	0.955	**52**	0.000	1.000	**79**	0.000	1.000	**106**	0.354	0.646	**133**	0.000	1.000	**160**	0.851	0.149
26	0.001	0.999	**53**	0.000	1.000	**80**	0.000	1.000	**107**	0.008	0.992	**134**	0.000	1.000	**161**	0.793	0.207
27	0.000	1.000	**54**	0.000	1.000	**81**	0.000	1.000	**108**	0.000	1.000	**135**	0.006	0.994	**162**	0.792	0.208

Table S4. Data matrix containing species information used in the analysis: Species name, subfamily, presence or absence of caudal luring (CL), conspicuous tail tip (CTT) and ontogenetic shift in diet (OSD) and bibliography used.

Species	**Subfamily**	**Caudal Luring (CL)**	**Conspicuous Tail Tip (CTT)**	**Ontogenetic Shift in Diet (OSD)**	**Reference (CL)**	**Reference (CTT)**	**Reference (OSD)**
Atheris barbouri	Viperinae		Não	Não		Rasmussen, J. B., & Howell, K. M. (1998).	Rasmussen, J. B., & Howell, K. M. (1998). Phelps, T. (2010).
Atheris matildae	Viperinae		Não			Menegon, M., Davenport, T. R., & Howell, K. M. (2011).	
Atheris ceratophora	Viperinae	Sim	Sim	Sim	Emmrich, D. (1997).	Emmrich, D. (1997).	Emmrich, D. (1997).
Atheris nitschei	Viperinae	Sim	Sim	Sim	Mallow, D., Ludwig, D., & Nilson, G. (2003).	Emmrich, D. (1997).) Mallow, D., Ludwig, D., & Nilson, G. (2003).	Broadley, D. G. (1998).
Atheris desaixi	Viperinae		Sim			Emmrich, D. (1997). Broadley, D. G. (1998). Mallow, D., Ludwig, D., & Nilson, G. (2003).	
Atheris hispida	Viperinae		Sim			https://www.inaturalist.org/observations/2667551	

						9 (acessado por último em 04/07/19 as 14h14)	
Atheris squamigera	Viperinae	Sim	Sim	Não	https://animaldiversity.org/accounts/Atheris_squamigera/#66665509-4145-4941-8C65-C70177620319 (último acesso em14/11/19 as 18h00)	Luiselli, L. (2000).	Luiselli, L. (2000).
Atheris chlorechis	Viperinae		Sim			Emmrich, D. (1997). Broadley, D. G. (1998). https://www.inaturalist.org/observations/9624221 (acessado por último em 04/07/19 as 14h14)	
Causus lichtensteinii	Viperinae	Não	Sim	Não	Coimbra, F. C. *et al.* (2018).	https://www.alamy.com/a-forest-night-adder-causus-lichtensteinii-	Ineich, I. *et al.* (2006). Vonesh, J. R. (2001).

						image279474437.html (último acesso 14/11/19 as 18h30)	
Causus rhombeatus	Viperinae	Não	Não	Não	https://lowvelder.co.za/wp-content/uploads/sites/44/2015/08/Rhombic-Night-Adder.pdf. (último acesso em 16/07/19 as 16h09) Coimbra, F. C. et al. (2018).	https://lowvelder.co.za/wp-content/uploads/sites/44/2015/08/Rhombic-Night-Adder.pdf. (último acesso em 16/07/19 as 16h09)	Mallow, D., Ludwig, D., & Nilson, G. (2003). https://lowvelder.co.za/wp-content/uploads/sites/44/2015/08/Rhombic-Night-Adder.pdf (último acesso em 16/07/19 as 16h09)
Causus resimus	Viperinae	Não		Não	Coimbra, F. C. *et al.* (2018).	Mallow, D., Ludwig, D., & Nilson, G. (2003). https://www.monaconatureencyclopedia.com/causus-resimus/?lang=en	

						(último acesso em 14/11/19 as 18h38)	
Causus defilippii	Viperinae	Não	Não	Não	Coimbra, F. C. et al. (2018).	Mallow, D., Ludwig, D., & Nilson, G. (2003).	Branch, B., (2001).
Proatheris superciliaris	Viperinae		Sim			Branch, B., (2001). Emmrich, D. (1997)	Branch, B., (2001).
Bitis arietans	Viperinae	Sim	Não	Sim	Glaudas, X. and Alexander, G.J., (2016)	Pauwels, O., Oger, M., Meirte, D. (2018). Phelps, T. (2010.	Phelps, T. (2010). Mallow, D., Ludwig, D., & Nilson, G. (2003). http://www.toxinology.com/fusebox.cfm?fuseaction=main.snakes.display&id=SN0200 (último acesso em 31/08/19 as 17h21)
Bitis worthingtoni	Viperinae		Sim			Phelps, T. (2010).	
Bitis parviocula	Viperinae		Sim			Phelps, T. (2010).	

						http://www.reptarium.cz/content/photo_rd_07/Bitis-parviocula-03000037317_01.jpg http://reptile-database.reptarium.cz/species?genus=Bitis&species=parviocula (ambos acessados por último 02/09/19 as 13h50)	
Bitis nasicornis	Viperinae		Não	Não		Pauwels, Olivier & Carlino, Piero & Chirio, Laurent & Meunier, Quentin & Vivien Okouyi Okouyi, Joseph & Orbell, Christopher & Rousseaux, Dominique & Testa, Olivier. (2017).	Luiselli, L., & Akani, G. C. (2003). Phelps, T. (2010).

Bitis gabonica	Viperinae		Não	Não		Mallow, D., Ludwig, D., & Nilson, G. (2003). https://animaldiversity.org/accounts/Bitis_gabonica/ (último acesso em 02/09/19 as 15h47)	Luiselli, L., & Akani, G. C. (2003).
Bitis peringueyi	Viperinae	Sim	Sim	Não	Reiserer, R. S., & DeNardo, D. F. (2000). FitzSimons, V. F. M. (1974) Mallow, D., Ludwig, D., & Nilson, G. (2003). Phelps, T. (2010).	Reiserer, R. S., & DeNardo, D. F. (2000). FitzSimons, V. F. M. (1974). Phelps, T. (2010).	Reiserer, R. S., & DeNardo, D. F. (2000). Branch, B., (2001).
Bitis schneideri	Viperinae	Sim	Sim	Não	Mallow, D., Ludwig, D., & Nilson, G. (2003). Phelps, T. (2010).	Mallow, D., Ludwig, D., & Nilson, G. (2003). Phelps, T. (2010). Reiserer, R. S., & DeNardo, D. F. (2000).	Maritz, B., & Alexander, G. J. (2014). Branch, B., (2001).

						https://www.inaturalist.org/observations/19447689 (último acesso em 04/09/19 as 11h41)	
Bitis caudalis	Viperinae	Sim	Sim	Não	Shine, R., Branch, W. R., Harlow, P. S., & Webb, J. K. (1998). FitzSimons, V. F. M. (1974). Phelps, T. (2010). Mallow, D., Ludwig, D., & Nilson, G. (2003).	Hoffmann, L. A. C. (1988). https://www.inaturalist.org/observations/15279467 https://www.inaturalist.org/observations/30500490 https://www.inaturalist.org/observations/21589252 (todos acessados por último em 04/09/19 as 10:25)	Shine, R., Branch, W. R., Harlow, P. S., & Webb, J. K. (1998). FitzSimons, V. F. M. (1974). Phelps, T. (2010).
Bitis atropos	Viperinae			Sim		https://www.inaturalist.org/observations/2471813	Phelps, T. (2010).

						6 (último acesso 04/09/19 as 12h06)	
Bitis armata	Viperinae		Não			https://www.africansnakebiteinstitute.com/articles/dwarf-adders-of-southern-africa/ (último acesso em 02/12/19 as 11h55)	
Bitis cornuta	Viperinae		Não	Não		https://www.inaturalist.org/observations/10828463 (último acesso em 05/09/19 as 14h55)	Branch, W. R. (1999).
Bitis rubida	Viperinae			Não			Mallow, D., Ludwig, D., & Nilson, G. (2003). Phelps, T. (2010). https://www.africansnakebiteinstitute.com/snake/red-adder/

							http://www.biodiversityexplorer.info/reptiles/squamata/serpentes/viperidae/bitis_rubida.htm (último acesso em 05/09/19 as 17h15)
Echis carinatus	Viperinae			Não			Barlow, A., Pook, C. E., Harrison, R. A., & Wüster, W. (2009). Rahman, H. (1993).
Echis coloratus	Viperinae			Não		Babocsay, G. (2003).	Barlow, A., Pook, C. E., Harrison, R. A., & Wüster, W. (2009).
Echis omanensis	Viperinae		Sim			Phelps, T. (2010).	
Echis pyramidum	Viperinae	Não		Não	Duff-Mackay, A. (1965).		Barlow, A., Pook, C. E., Harrison, R. A., & Wüster, W. (2009).

Echis jogeri	Viperinae		Não			https://www.flickr.com/photos/64374409@N05/31116479016 (último acesso em 09/09/19 as 11h30)	
Echis ocellatus	Viperinae			Não			Barlow, A., Pook, C. E., Harrison, R. A., & Wüster, W. (2009).
Cerastes gasperettii	Viperinae	Sim	Sim		Young, B. A., & Morain, M. (2002).	Mallow, D., Ludwig, D., & Nilson, G. (2003).	
Cerastes cerastes	Viperinae	Sim	Sim		Young, B. A., & Morain, M. (2002).	Mallow, D., Ludwig, D., & Nilson, G. (2003). https://animaldiversity.org/accounts/Cerastes_cerastes/ https://en.wikipedia.org/wiki/Cerastes_cerastes (último acesso em 09/09/19 as 18h04)	

						https://www.inaturalist.org/observations/31365783 https://www.inaturalist.org/observations/21462732 (último acesso em 10/09/19 as 16h14)	
Cerastes vipera	Viperinae	Sim	Sim	Não	Mallow, D., Ludwig, D., & Nilson, G. (2003). Heatwole, H., & Davison, E. (1976). https://www.reptiletalk.net/sahara-sand-viper/ (último acesso em 10/09/19 as 18h46)	Phelps, T. (2010). Heatwole, H., & Davison, E. (1976).	Heatwole, H., & Davison, E. (1976).
Pseudocerastes urarachnoides	Viperinae	Sim	Sim		Fathinia, B. *et al.* (2015).	Fathinia, B. et al. (2015).	

						del Marmol, G. M., Mozaffari, O., & Gállego, J. (2016).	
Pseudocerastes persicus	Viperinae		Sim	Não		del Marmol, G. M., Mozaffari, O., & Gállego, J. (2016). Mallow, D., Ludwig, D., & Nilson, G. (2003).	Khan, M. S. (2002). A guide to the snakes of Pakistan (Vol. 16). Frankfurt am Main: Edition Chimaira.
Pseudocerastes fieldi	Viperinae		Sim			del Marmol, G. M., Mozaffari, O., & Gállego, J. (2016). https://www.inaturalist.org/observations/27219492 (último acesso em 11/09/19 as 11h00)	
Eristicophis macmahoni	Viperinae	Sim	Sim		https://www.youtube.com/watch?v=ykOyp85jvqE (último acesso em 04/12/19 as 21h17) ->	https://www.inaturalist.org/observations/147745 https://en.wikipedia.org/wiki/Eristicophis (último	

					COMUNICAÇÃO PESSOAL REUBER BRANDÃO (ID DA ESPECIE CORRETA)	acesso em 15/11/19 as 11h40)	
Vipera nikolskii	Viperinae		Sim			Phelps, T. (2010). David, P., & Vogel, G. (2010). Milto, K. D., & Zinenko, O. I. (2005).	
Vipera berus	Viperinae		Sim	Sim		Mallow, D., Ludwig, D., & Nilson, G. (2003). Parellada, X., & Santos, X. (2002).	Girons, H. S. (1980). Mallow, D., Ludwig, D., & Nilson, G. (2003).
Vipera barani	Viperinae		Sim			Mallow, D., Ludwig, D., & Nilson, G. (2003). Baran, İ., Joger, U., Kutrup, B., & Türkozan, O. (2001).n the Middle East, 23(1), 47–53.	

						Böhme, W., & Joger, U. (1983).	
Vipera seoanei	Viperinae		Sim	Sim		Parellada, X., & Santos, X. (2002). Bea, A., Bas, S., Braña, F., & Girons, H. (1984).	Girons, H. S. (1980). Brana, F., Bea, A., & Saint Girons, H. (1988).
Vipera kaznakovi	Viperinae		Sim	Sim		https://viperacaucasica.wordpress.com/kaznakovi/ https://www.stlzoo.org/animals/abouttheanimals/reptiles/snakes/caucasusviper (último acesso em 12/09/19 as 17h53)	Phelps, T. (2010). Mallow, D., Ludwig, D., & Nilson, G. (2003). Girons, H. S. (1980).
Vipera orlovi	Viperinae		Sim			Tuniyev, B. S., & Ostrovskikh, S. V. (2001).	
Vipera ursinii	Viperinae		Não	Sim		Phelps, T. (2010). Nilson, G., & Andren, C. (1988	Baron, J. P. (1992). Conservation effort to save Hungarian

							meadow viper (Vipera ursinii rakosiensis) from extinction: https://ec.europa.eu/environment/nature/natura2000/management/docs/Vipera%20ursinii%20factsheet%20-%20SWIFI.pdf https://ec.europa.eu/environment/nature/natura2000/awards/previous-editions/2015-edition/applications/conservation/index_en.htm Official webpage of the Hungarian meadow viper Life-

							project: https://www.rakosivipera.hu/en/ (todos os links último acesso em15/11/19 as 14h09)
Vipera dinniki	Viperinae		Não	Sim		Orlov,N.L. & B.S. Tuniyev. 1990.	Phelps, T. (2010). Mallow, D., Ludwig, D., & Nilson, G. (2003). Orlov,N.L. & B.S. Tuniyev. 1990. https://viperacaucasica.wordpress.com/dinniki/ (último acesso em 15/11/19 as 13h05)
Vipera renardi	Viperinae		Não	Sim		David, P., & Vogel, G. (2010).	Girons, H. S. (1980). https://uk.wikipedia.org/wiki/Гадюка_степова (último acesso em 23/09/19 as 16h16)

Vipera anatolica	Viperinae		Sim	Não		Göçmen, B. *et al.* (2017).	Göçmen, B. et al. (2017). Zinenko *et al.* (2016). Göçmen *et al.* (2014).
Vipera aspis	Viperinae		Sim	Sim	Parellada, X., & Santos, X. (2002).	Mallow, D., Ludwig, D., & Nilson, G. (2003). Parellada, X., & Santos, X. (2002).	Mallow, D., Ludwig, D., & Nilson, G. (2003). Girons, H. S. (1980).
Vipera latastei	Viperinae	Sim	Sim	Sim	Parellada, X., & Santos, X. (2002).	Parellada, X., & Santos, X. (2002). David, P., & Vogel, G. (2010).	Bea, A., Braña, F. (1988).
Vipera transcaucasiana	Viperinae		Sim			Phelps, T. (2010). David, P., & Vogel, G. (2010). Kutrup, B. (1999).	
Vipera ammodytes	Viperinae	Sim	Sim	Sim	Zadravec, M. (2014).	Phelps, T. (2010). Parellada, X., & Santos, X. (2002).	Girons, H. S. (1980). Mallow, D., Ludwig, D., & Nilson, G. (2003).

						David, P., & Vogel, G. (2010).	
Daboia mauritanica	Viperinae		Sim	Sim	Martínez, G., & León, R. (2013). http://www.moroccoherps.com/en/ficha/Daboia_mauritanica/ (último acesso em 24/09/19 as 10h41)	Gabriel Martínez del Mármol Marín (2013).	Phelps, T. (2010).
Daboia deserti	Viperinae			Sim			Phelps, T. (2010).
Daboia palaestinae	Viperinae			Sim			Phelps, T. (2010).
Daboia siamensis	Viperinae	Sim	Sim	Sim	http://herpingthailand.com/snakes-of-thailand/vipers/daboia-siamensis-siamese-russells-viper/ (último acesso em 24/09/19 as 18h07) personal	Phelps, T. (2010).	Phelps, T. (2010). http://herpingthailand.com/snakes-of-thailand/vipers/daboia-siamensis-siamese-russells-viper/ (último acesso em 24/09/19 as 18h07)

					communication Parinya Pawangkhanant		
Macrovipera schweizeri	Viperinae		Sim	Sim		Phelps, T. (2010).	Phelps, T. (2010). Nilson, G. *et al.* (1999).
Macrovipera lebetina	Viperinae		Sim	Sim		https://en.wikipedia.org/wiki/Macrovipera_lebetina_obtusa#/media/File:Macrovipera_lebetina_obtusa01.jpg https://de.wikipedia.org/wiki/Levanteotter https://www.inaturalist.org/observations/12962330 (último acesso em 15/11/19 as 14h50)	Phelps, T. (2010). David, P., & Vogel, G. (2010).
Montivipera latifii	Viperinae			Sim			Phelps, T. (2010).

Montivipera raddei	Viperinae		Não	Sim		David, P., & Vogel, G. (2010).	Phelps, T. (2010). Mallow, D., Ludwig, D., & Nilson, G. (2003). https://de.wikipedia.org/wiki/Armenische_Bergotter (último acesso em 24/09/19 as 19h39)
Montivipera albizona	Viperinae		Não			Oğuz, M. *et al.* (2017).	
Montivipera xanthina	Viperinae		Sim	Sim		http://en.balcanica.info/2-8747 http://en.balcanica.info/2-8750 http://en.balcanica.info/2-5929 (último acesso em 15/11/19 as 15h48)	Jablonski, D., Zerzán, D., & Çiçek, K. (2015).
Trimeresurus malabaricus	Crotalinae		Sim	Sim		Sagar, U. (2016).	Sagar, U. (2016).

						https://www.inaturalist.org/observations/29107971 (último acesso em 25/09/19 as 15h00). Vogel, G. (2006).	
Trimeresurus gramineus	Crotalinae		Sim			Neill, W. T. (1960).	
Trimeresurus trigonocephalus	Crotalinae		Sim	Sim		https://en.wikipedia.org/wiki/Trimeresurus_trigonocephalus (último acesso em 25/09/19 as 17h18)	https://www.acq.osd.mil/eie/afpmb/docs/lhd/venomous_animals_byspecies.pdf (último acesso em 25/09/19 as 16h58)
Trimeresurus puniceus	Crotalinae		Sim	Não		Neill, W. T. (1960). https://www.reptiletalk.net/flat-nosed-pitviper/ (último acesso em 26/09/19 as 15h52)	Orlov, N., Ananjeva, N., & Khalikov, R. (2002).
Trimeresurus borneensis	Crotalinae		Sim			Neill, W. T. (1960).	

						https://www.inaturalist.org/observations/24218134 (último acesso em 26/09/19 as 16h21)	
Trimeresurus hageni	Crotalinae		Sim			Vogel, G. (2006). http://reptile-database.reptarium.cz/species?genus=Trimeresurus&species=hageni https://www.gbif.org/species/2444189 https://www.inaturalist.org/observations/1381020 https://www.mybis.gov.my/sp/9931 (último acesso em 26/09/19 as 16h45)	https://www.ecologyasia.com/verts/snakes/hagen%27s-pit-viper.htm https://www.iucnredlist.org/species/191906/2013598#habitat-ecology (último acesso em 26/09/19 as 16h40)
Trimeresurus schultzei	Crotalinae		Sim			Vogel, G. (2006). https://www.inaturalist.org/observations/3648773	

						(ambos links último acesso em 15/11/19 as 16h51)	
Trimeresurus sumatranus	Crotalinae		Sim			Neill, W. T. (1960). Vogel G, David P, Sidik I. 2014. Vogel, G. (2006). https://en.wikipedia.org/wiki/Trimeresurus_sumatranus http://reptile-database.reptarium.cz/species?genus=Trimeresurus&species=sumatranus (último acesso em 26/09/19 as 17h07)	https://www.acq.osd.mil/eie/afpmb/docs/lhd/venomous_animals_byspecies.pdf (último acesso em 26/09/19 as 17h16)
Trimeresurus flavomaculatus	Crotalinae		Sim	Não		Vogel, G. (2006). https://www.inaturalist.org/observations/2146915	Sanders, K. L., Malhotra, A., & Thorpe, R. S. (2004).

						9 (último acesso em 30/09/19 as 14h57)	https://www.iucnredlist.org/species/169885/6686236#habitat-ecology (último acesso em 30/09/19 as 15h52)
Trimeresurus malcolmi	Crotalinae		Sim			https://www.inaturalist.org/observations/11429662 (último acesso em 30/09/19 as 16h35)	
Trimeresurus septentrionalis	Crotalinae		Sim			Vogel, G. (2006). http://reptile-database.reptarium.cz/species?genus=Trimeresurus&species=septentrionalis	
Trimeresurus erythrurus	Crotalinae		Sim	Sim		Neill, W. T. (1960). https://www.indianreptiles.org/sp/512/Trimeresurus-erythrurus (último	Orlov, N., Ananjeva, N., & Khalikov, R. (2002).

						acesso em 30/09/19 as 17h13)	
Trimeresurus albolabris	Crotalinae		Sim			Neill, W. T. (1960). https://en.wikipedia.org/wiki/Trimeresurus_albolabris#/media/File:Trimeresurus_albolabris_male.jpg (último acesso em 01/10/19 as 16h40)	Orlov, N., Ananjeva, N., & Khalikov, R. (2002). https://ultimateexotics.co.za/white-lipped-tree-viper-caresheet-trimeresurus-albolabris/ (último acesso em 01/10/19 as 18h00)
Trimeresurus fasciatus	Crotalinae		Não			David, P., Vogel, G., & Vidal, N. (2003).	
Trimeresurus insularis	Crotalinae	Não	Sim		Trimeresurus insularis (White-lipped Island Pit Viper) Foraging behavior and diet,	Vogel, G. (2006). https://alephrocco.wordpress.com/2018/05/02/white-lipped-island-pit-viper-	

					Sean, B. Reilly et al., 2016	trimeresurus-insularis/ https://alephrocco.wordpress.com/2018/05/31/young-blue-insular-pit-viper-trimeresurus-insularis/ https://www.inaturalist.org/taxa/146509-Trimeresurus-insularis/browse_photos (último acesso em 01/10/19 as 17h48)	
Trimeresurus kanburiensis	Crotalinae		Não			Malhotra, A., & Thorpe, R. S. (2004).	https://en.wikipedia.org/wiki/Trimeresurus_kanburiensis http://herpingthailand.com/snakes-of-

							thailand/vipers/trimeresurus-kanburiensis-kanburi-pit-viper/ (último acesso em 02/10/19 as 11h03)
Trimeresurus venustus	Crotalinae		Sim			David, P., Vogel, G., Sumontha, M., Pauwels, O. S., & Chanhome, L. (2004).	
Trimeresurus macrops	Crotalinae		Sim	Não	Strine, C., Silva, I., Barnes, C. H., Marshall, B. M., Artchawakom, T., Hill, J., & Suwanwaree, P. (2018).	https://www.thainationalparks.com/species/trimeresurus-macrops (último acesso em 20/11/19 as 10h11) Malhotra, A., Thorpe, R. S., & Stuart, B. L. (2011).	Orlov, N., Ananjeva, N., & Khalikov, R. (2002).
Trimeresurus medoensis	Crotalinae		Sim		David, P., Captain, A., & Bhatt, B. B. (2001).	Vogel, G. (2006). https://www.asian-pitvipers.com/wp-	

						content/uploads/2017/06/Viridovipera-medoensis-Soham-Mukherjee.jpg http://indiansnakes.org/content/medo-pit-viper (último acesso em 02/10/19 as 14h55) David, P., Captain, A., & Bhatt, B. B. (2001).	
Trimeresurus yunnanensis	Crotalinae		Sim			Vogel, G. (2006).	
Trimeresurus stejnegeri	Crotalinae		Sim	Não		Vogel, G. (2006). Neill, W. T. (1960). http://www.gondwanareptileproductions.com/tstejnegeri.jpg (último acesso em 25/09/19 as 16h54)	Orlov, N., Ananjeva, N., & Khalikov, R. (2002). - Strine, C. *et al.* (2018). Creer, S., Chou, W. H., Malhotra, A., & Thorpe, R. S. (2002).

Trimeresurus gumprechti	Crotalinae		Sim			Vogel, G. (2006). https://www.thainationalparks.com/species/trimeresurus-gumprechti (último aceso em 03/10/19 as 11h41) David, P., Vogel, G., Pauwels, O. S., & Vidal, N. (2002).	
Trimeresurus truongsonensis	Crotalinae		Sim			Das, I. (2015).	
Trimeresurus vogeli	Crotalinae		Não			Malhotra, A., Thorpe, R. S., & Stuart, B. L. (2004). https://www.ecologyasia.com/verts/snakes/vogels-green-pit-viper.htm https://www.inaturalist.org/observations/24396605	Malhotra, A., Thorpe, R. S., & Stuart, B. L. (2004).

						https://www.inaturalist.org/observations/2431745 (último acesso em 03/10/19 as 14h56)	
Trimeresurus sichuanensis	Crotalinae		Sim			http://reptile-database.reptarium.cz/species?genus=Trimeresurus&species=sichuanensis (último acesso em 03/10/19 as 15h15) Qin, L. *et al.* (2014).	
Trimeresurus sabahi	Crotalinae		Sim			http://reptile-database.reptarium.cz/species?genus=Trimeresurus&species=sabahi (último acesso em 03/10/19 as 16h20) Vogel, G., David, P., & Pauwels, O. S. (2004).	

Trimeresurus popeiorum	Crotalinae	Sim	Sim		Herping Thailand personal communication (email)	Neill, W. T. (1960). https://www.thainationalparks.com/species/trimeresurus-popeiorum (último acesso em 04/10/19 as 14h51) Vogel, G., David, P., & Pauwels, O. S. (2004).	
Trimeresurus nebularis	Crotalinae		Sim			https://www.thainationalparks.com/species/trimeresurus-nebularis (último acesso em 04/10/19 as 15h06) Vogel, G., David, P., & Pauwels, O. S. (2004).	
Trimeresurus tibetanus	Crotalinae		Não			David, P., & Tong, H. (1997).	

Lachesis melanocephala	Crotalinae		Sim	Não		Ripa, D. (2001).	Ripa, D. (2001).
Lachesis stenophrys	Crotalinae		Sim	Não		Ripa, D. (2001).	Ripa, D. (2001).
Lachesis muta	Crotalinae	Não	Sim	Não	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Ripa, D. (2001).	Ripa, D. (2001).
Lachesis acrochorda	Crotalinae		Sim	Não		Ripa, D. (2001).	Ripa, D. (2001).
Sistrurus catenatus	Crotalinae	Sim	Sim	Sim	https://animaldiversity.org/accounts/Sistrurus_catenatus/ Schuett, G. W.; Clark, D. L.; Kraus, F. (1984).	https://nature.mdc.mo.gov/discover-nature/field-guide/prairie-massasauga (último acesso em 23/05 às 14:45)	Holycross, A. T., & Mackessy, S. P. (2002).
Sistrurus miliarius	Crotalinae	Sim	Sim	Sim	Rabatsky, A. M., & Waterman, J. M. (2005).	Farrell, T. M., May, P. G., & Andreadis, P. T. (2011).	https://animaldiversity.org/accounts/Sistrurus_miliarius/#1A804BA6-7886-11E6-

					https://animaldiversity.org/accounts/Sistrurus_miliarius/ https://srelherp.uga.edu/snakes/sismil.htm https://en.wikipedia.org/wiki/Sistrurus_miliarius		8505-A820662394EA (último acesso em 25/05 às 15:10)
Crotalus pricei	Crotalinae	Não	Não	Não	Prival, D. B., & Schroff, M. J. (2012). http://www.reptilesofaz.org/Snakes-Subpages/h-c-pricei.htm	Prival, D. B., & Schroff, M. J. (2012).	Prival, D. B., & Schroff, M. J. (2012).
Crotalus adamanteus	Crotalinae		Não	Não	https://animaldiversity.org/accounts/Crotalus_adamanteus/ (último acesso em 23/05 às 14:50)	http://reptile-database.reptarium.cz/species?genus=Crotalus&species=adamanteus (último acesso em 23/05 às 14:51)	https://en.wikipedia.org/wiki/Eastern_diamondback_rattlesnake (último acesso em 23/05 às 15:11)

Crotalus mitchellii	Crotalinae		Não	Não	http://www.reptilesofaz.org/Snakes-Subpages/h-c-mitchellii.html Strimple, Pete 1992. http://www.redtox.org/crotalus-mitchelli (último acesso 23/05 às 15:13)	http://www.californiaherps.com/noncal/baja/bajasnakes/images/cmmitchelliibcswf815.jpg (último acesso 23?05 às 15:13)	Meik, J. M., *et al.* (2012).
Crotalus tigris	Crotalinae		Não	Sim		http://www.reptilesofaz.org/Snakes-Subpages/h-c-tigris.html (último acesso 23/05 às 14:56)	Calvete, J. J. *et al.* (2012).
Crotalus scutulatus	Crotalinae		Sim	Sim		http://www.californiaherps.com/snakes/images/csscutulatussccoaz.jpg (último acesso em 23/05 às 14:58)	http://explorer.natureserve.org/servlet/NatureServe?sourceTemplate=tabular_report.wmt&loadTemplate=species_RptComprehensive.wmt&selectedRe

							port=RptComprehensive.wmt&summaryView=tabular_report.wmt&elKey=100052&paging=home&save=true&startIndex=1&nextStartIndex=1&reset=false&offPageSelectedElKey=100052&offPageSelectedElType=species&offPageYesNo=true&post_processes=&radiobutton=radiobutton&selectedIndexes=100052&selectedIndexes=103083 (último acesso 23:05 às 15:15)

Crotalus cerberus	Crotalinae		Não	Não		http://www.reptilesofaz.org/Graphics/Snakes/CROCERB-5.jpg https://tucsonherpsociety.org/wp-content/uploads/2018/08/CRCE_Yearling_Pic021.jpg (último acesso 23?05 às 15:16)	Loughran, C.L., Nowak, E.M. and Parker, R.W., 2012. https://tucsonherpsociety.org/amphibians-reptiles/snakes/arizona-black-rattlesnake-2/
Crotalus oreganus	Crotalinae	Não	Não	Sim	Parker, J.M. and Anderson, S.H., 2007.	http://www.californiaherps.com/snakes/images/cooreganussols4142.jpg (último acesso 23/05 às 15:17)	Glaudas, X., Jezkova, T., & Rodríguez-Robles, J. A. (2008). Parker, J.M. and Anderson, S.H., (2007). Mackessy, S.P., (1988).
Crotalus viridis	Crotalinae		Não	Sim		http://reptile-database.reptarium.cz/species?genus=Crotalus&s	Saviola, A.J., Chiszar, D. and Mackessy, S.P., (2012).

						pecies=viridis último (acesso 23/05 às 15:18)	
Crotalus ruber	Crotalinae		Sim	Não		http://www.californiaherps.com/snakes/images/cruberjuvsdcowdc1118.jpg (último acesso 25/05 às 15H19)	Dugan, E. A., & Hayes, W. K. (2012). Avila-Villegas, H., Martins, M., & Arnaud, G. (2007).
Crotalus atrox	Crotalinae		Sim			http://www.reptilesofaz.org/Snakes-Subpages/h-c-atrox.html (último acesso 23/05 às 15:21)	Beavers, R.A., (1976). https://en.wikipedia.org/wiki/Western_diamondback_rattlesnake
Crotalus catalinensis	Crotalinae		Sim	Sim		Beaman, K. R. & Wong, N. (2001).	Avila-Villegas, H., Martins, M., & Arnaud, G. (2007).
Crotalus willardi	Crotalinae	Sim	Sim	Sim	Holycross, A.T., Painter, C.W., Barker, D.G. and	https://tucsonherpsociety.org/wp-content/uploads/2018/08/AZ-ridge-nosed-	Holycross, A.T., Painter, C.W., Barker, D.G. and Douglas, M.E. (2002).

					Douglas, M.E., (2002). Setser, K., Mociño-Deloya, E., & Meik, J. M. (2011). https://tucsonherpsociety.org/amphibians-reptiles/snakes/ridge-nosed-rattlesnake/	rattlesnake-juv3-W-side-Huachucas-A15-1024x831.jpG https://tucsonherpsociety.org/amphibians-reptiles/snakes/ridge-nosed-rattlesnake/ (ambos acessados por último em 21/05/2019 as 14h09) Holycross, A.T., Painter, C.W., Barker, D.G. and Douglas, M.E., (2002).	Mociño-Deloya, E., *et al.* (2015).
Crotalus tzabcan	Crotalinae		Não			https://www.inaturalist.org/observations/19667336	
Crotalus durissus	Crotalinae	Não	Não	Não	Hoyos, M. A., & Almeida-Santos, S. M. (2016).	https://animaldiversity.org/accounts/Crotalus_durissus/pictures/collections/contributors/jairo_mal	Hoyos, M. A., & Almeida-Santos, S. M. (2016).

					Sueiro, L.R. & de Campos Brites, V.L., (2006). Goode, M. *et al.* (1990).	donado/Crotalus_durissus/ https://www.inaturalist.org/taxa/30693-Crotalus-durissus/browse_photos	Salomão, M.D., Santos, S.M.A. & Puorto, G. (1995).
Crotalus molossus	Crotalinae		Sim	Sim		https://tucsonherpsociety.org/amphibians-reptiles/snakes/black-tailed-rattlesnake/ (acessado por último em 21/05/19 as 14h31)	Balderas-Valdivia, C.J., Barreto-Oble, D. & Madrid-Sotelo, C.A. (2009).
Crotalus basiliscus	Crotalinae		Não			https://www.inaturalist.org/observations/19717180 (acessado por último em 21/05/19 as 14h35) Loc-Barragán, J. A., Carbajal-Márquez, R. A., Woolrich-Piña, G. A.	

						& Navarro-Orozco, R. R. (2016).	
Crotalus totonacus	Crotalinae		Sim	Não		Farr, W. L., Nevárez-De Los Reyes, M., Lazcano, D. & Ortiz-Hernández, S. E. (2015). https://www.inaturalist.org/observations/13955212	Ernst, C. H., & Ernst, E. M. (2011).
Crotalus ornatus	Crotalinae		Sim	Sim		https://www.inaturalist.org/taxa/503374-Crotalus-ornatus/browse_photos https://www.inaturalist.org/observations/19668036 ambos acessados por (último em 21/05/19 as 15h04)	Lazcano-Villareal, D. (2017)

Crotalus horridus	Crotalinae	Não	Sim	Não	Reinert, H.K. *et al*. (2011). Clark, R. W. (2006).	https://www.inaturalist.org/taxa/30746-Crotalus-horridus/browse_photos https://www.inaturalist.org/observations/25300328 ambos acessados por (último em 21/05/19 as 15h33)	Reinert, H.K. *et al*. (2011). Clark, R. W. (2006).
Crotalus lannomi	Crotalinae		Não			Reyes-Velasco, J. *et al*. (2010).	
Crotalus ericsmithi	Crotalinae		Não			Campbell, J. A., & Flores-Villela, O. (2008).	
Crotalus aquilus	Crotalinae		Sim	Não		https://www.inaturalist.org/taxa/73723-Crotalus-aquilus/browse_photos https://www.inaturalist.org/observations/1910725 (ambos acessados por	Mociño-Deloya, M. E. (2016). Mociño-Deloya, E., Setser, K., Peurach, S.C. & Meik, J.M., (2008).

						último em 21/05/19 as 16h11)	
Crotalus lepidus	Crotalinae	Sim	Sim	Não	Starrett, B. L., AND Holycross, A. T. (2000). Mociño-Deloya, M. E. (2016). https://tucsonherpsociety.org/amphibians-reptiles/snakes/rock-rattlesnake/ Holycross, A. T. *et al.* (2002).	Holycross, A. T. *et al.* (2002).	Holycross, A. T. *et al.* (2002).
Crotalus triseriatus	Crotalinae		Sim	Sim		https://www.inaturalist.org/observations/6611578 (acessado por último em 21/05/19 as 18h13)	Mociño-Deloya, E., Setser, K., & Pérez-Ramos, E. (2014).
Crotalus ravus	Crotalinae		Sim			https://www.inaturalist.org/observations/22335152	Domínguez-Godoy, M. A., R. Barrios-Montiel, A. Bautista,

						https://www.inaturalist.org/observations/4964558 (ambos acessados por último em 21/05/19 as 18h58)	& Díaz de La Vega-Pérez, A. H. (2017). Díaz de la Vega-Pérez, A. H. *et al.* (2016).
Crotalus cerastes	Crotalinae	Sim	Sim	Sim	Reiserer, R. S., & Schuett, G. W. (2008). https://www.youtube.com/watch?v=N2Nf8uMOZ2c	http://www.californiaherps.com/snakes/pages/c.c.cerastes.html (acessado por último em 23/05/19 as 14h51)	Webber, M.M., Jezkova, T. & Rodríguez-Robles, J.A., (2016). http://www.californiaherps.com/snakes/pages/c.c.cerastes.html (acessado por último em 21/05/19 as 21h59)
Crotalus polystictus	Crotalinae	Não	Não	Não	Mociño-Deloya, M. E. (2016).	https://www.inaturalist.org/taxa/30761-Crotalus-polystictus/browse_photos	Mackessy, S. *et al.* (2018). Mociño-Deloya, M. E. (2016).

Crotalus enyo	Crotalinae		Não	Sim		https://www.inaturalist.org/observations/17949447 (último acesso 23/05/19 as 19h11)	Emily N. Taylor (2001).
Agkistrodon piscivorus	Crotalinae	Sim	Sim	Sim	Eskew, E.A., Willson, J.D. & Winne, C.T. (2009). Wharton, C. H. (1960). Reiserer, R. S., & Schuett, G. W. (2008).1.	Eskew, E.A., Willson, J.D. & Winne, C.T. (2009).	Eskew, E.A., Willson, J.D. & Winne, C.T. (2009).
Agkistrodon taylori	Crotalinae	Sim	Sim		O'Shea, M. (1998). Lomonte, B. *et al.* (2014). https://nationalzoo.si.edu/animals/taylors-cantil https://en.wikipedia.org/wiki/Agkistrodo	Porras, L. W., Wilson, L. D., Schuett, G. W., & Reiserer, R. S. (2013). http://reptile-database.reptarium.cz/species?genus=Agkistrodon&species=taylori	

					n_taylori (ambos os sites: último acesso 23/05/19 as 19h41)	https://en.wikipedia.org/wiki/Agkistrodon_taylori#/media/File:Agkistrodon_taylori.jpg (último acesso em 23/05/19 as 22h15) Burchfield, P. M. (1982).	
Agkistrodon howardgloydi	Crotalinae	Sim	Sim	Sim	http://icp.ucr.ac.cr/en/information-and-materials/venomous-snakes-costa-rica/agkistrodon-howardgloydi (acessado em 23/05/19 - 22h19)	http://reptile-database.reptarium.cz/species?genus=Agkistrodon&species=howardgloydi (último acesso em 23/05/19 as 22h17)	Solorzano, A., Romero, M., Gutierrez, J. M., & Sasa, M. (1999). Lomonte, B. et al. (2014).
Agkistrodon russeolus	Crotalinae		Sim			Porras, L. W., Wilson, L. D., Schuett, G. W., & Reiserer, R. S. (2013).8-73.	

Agkistrodon bilineatus	Crotalinae	Sim	Sim	Sim	Smetsers, P. (1993). http://www.toxinology.com/fusebox.cfm?fuseaction=main.snakes.display&id=SN0326 (acessado em 23/05/19 as 22h24)	Arenas-Monroy, J. C., & Ahumada-Carrillo, I. T. (2015). Porras, L. W., Wilson, L. D., Schuett, G. W., & Reiserer, R. S. (2013).	Lomonte, B. et al. (2014).
Agkistrodon contortrix	Crotalinae	Sim	Sim	Sim	Neill, W. T. (1960). https://animaldiversity.org/accounts/Agkistrodon_contortrix/ (último acesso em 23/05/19 as 22h30) Conant, R. & Collins, J. (1998). Reiserer, R. S. (2002).	Neill, W. T. (1960).	Lomonte, B. et al. (2014). Reiserer, R. S. (2002).
Bothrocophias hyoprora	Crotalinae		Sim	Sim		Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).

							Bernarde, P. S., Amaral, E. S. & Vale, M. A. D. (2011). Carvalho, V. T. *et al.* (2013).
Bothrops ammodytoides	Crotalinae		Sim	Não	Carrasco, P. A., Leynaud, G. C., & Scrocchi, G. J. (2010).	Martins, M., Marques, O. A., & Sazima, I. (2002). Carrasco, P. A., Leynaud, G. C., & Scrocchi, G. J. (2010).	de Roodt, A. R. (2016).
Bothrops alternatus	Crotalinae	Não	Não	Não	Nunes, S. D. F., Kaefer, I. L., Leite, P. T., & Cechin, S. Z. (2010). Nunes, S. D. F. (2006).	Martins, M., Marques, O. A., & Sazima, I. (2002). Liberato, C. W. (2010).	Nunes, S. D. F., Kaefer, I. L., Leite, P. T., & Cechin, S. Z. (2010).
Bothrops fonsecai	Crotalinae	Não	Sim	Não	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). -

							Liberato, C. W. (2010). Tashima, A. K. *et al.* (2008).
Bothrops cotiara	Crotalinae	Não	Não	Não	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Liberato, C. W. (2010). Tashima, A. K. et al. (2008).
Bothrops itapetiningae	Crotalinae	Não	Sim	Não	Leão, S. M. (2012). Leão, S. M., Pelegrin, N., de Campos Nogueira, C., & Brandão, R. A. (2014).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Leão, S. M., Pelegrin, N., de Campos Nogueira, C., & Brandão, R. A. (2014).

Bothrops insularis	Crotalinae	Sim	Sim	Sim	Andrade, D. V. *et al.* (2010).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Andrade, D. V. *et al.* (2010).
Bothrops jararaca	Crotalinae	Sim	Sim	Sim	Sazima, I. (2006). Hartmann, P. A., Hartmann, M. T., & Giasson, L. O. M. (2003).	Sazima, I. (2006). Martins, M., Marques, O. A., & Sazima, I. (2002).	Sazima, I. (1992). Martins, M., Marques, O. A., & Sazima, I. (2002).
Bothrops alcatraz	Crotalinae	Não	Não	Não	Marques, O. A., Martins, M., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Marques, O. A., Martins, M., & Sazima, I. (2002).	Marques, O. A., Martins, M., & Sazima, I. (2002).
Bothrops matogrossensis	Crotalinae		Sim	Não		Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Monteiro, C., Montgomery, C. E., Spina, F., Sawaya, R.

							J., & Martins, M. (2006).
Bothrops pauloensis	Crotalinae		Sim	Sim		Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Valdujo, P. H., Nogueira, C., & Martins, M. (2002).
Bothrops pubescens	Crotalinae	Sim	Sim	Sim	Hartmann, M. T., Hartmann, P. A., Cechin, S. Z., & Martins, M. (2005).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Hartmann, M. T., Hartmann, P. A., Cechin, S. Z., & Martins, M. (2005).
Bothrops diporus	Crotalinae	Não	Sim	Não	Giraudo, A. R. *et al.* (2008). Rocha, M. C. D. (2010). Teixeira, L. F., & Zuliani, J. P. (2014). Liberato, C. W. (2010).	Liberato, C. W. (2010).	Liberato, C. W. (2010).

Bothrops erythromelas	Crotalinae		Sim	Não		Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).
Bothrops neuwiedi	Crotalinae		Sim	Não		Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).
Bothrops marmoratus	Crotalinae		Sim			http://reptile-database.reptarium.cz/species?genus=Bothrops&species=marmoratus (último acesso em 23/05/19 as 23h20)	
Bothrops caribbaeus	Crotalinae		Sim	Não		Powell, R., & Wittenberg, R. D. (1998). Hadley, W. F., & Gans, C. (1972).	Henderson, R. W. (2004).
Bothrops lanceolatus	Crotalinae			Não			Henderson, R. W. (2004).

Bothrops asper	Crotalinae	Sim	Sim	Sim	Tryon, B. W. (1985). Sasa, M., Wasko, D. K., & Lamar, W. W. (2009).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Sasa, M., Wasko, D. K., & Lamar, W. W. (2009). Campbell, J. A. (1999).
Bothrops atrox	Crotalinae	Sim	Sim	Sim	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Bernarde, P. S. (2012).	Martins, M., Marques, O. A., & Sazima, I. (2002). Gonçalves Bisneto, P. F. (2016).
Bothrops leucurus	Crotalinae	Sim	Sim	Sim	de Freitas, Marco António and Thaís Figueiredo Santos Silva. 2011. Martins, M., Marques, O. A. V., Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). Lira-da-Silva, R. M. (2009).	Martins, M., Marques, O. A., & Sazima, I. (2002). Lira-da-Silva, R. M. (2009).

					Lira-da-Silva, R. M. (2009).		
Bothrops moojeni	Crotalinae	Sim	Sim	Sim	Martins, M., Marques, O. A., & Sazima, I. (2002). Andrade, D. V., Abe, A. S., & Dos Santos, M. C. (1996).	Martins, M., Marques, O. A., & Sazima, I. (2002). Nogueira, C., Sawaya, R. J., & Martins, M. (2003).	Martins, M., Marques, O. A., & Sazima, I. (2002). Nogueira, C., Sawaya, R. J., & Martins, M. (2003).
Bothrops osbornei	Crotalinae	Sim	Sim		Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	https://www.inaturalist.org/observations/17052181 (último acesso em 23/05 às 15:03) Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).
Bothrops punctatus	Crotalinae	Sim	Sim	Sim	Ospina-L, A. M. (2017). Arteaga, A., L. Bustamante y J. M. Guayasamin. (2013).	Ospina-L, A. M. (2017).	Arteaga, A., L. Bustamante y J. M. Guayasamin. (2013).

Bothrops brazili	Crotalinae		Sim	Sim	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Martins, M., Marques, O. A., & Sazima, I. (2002). Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Martins, M., Marques, O. A., & Sazima, I. (2002).
Bothrops jararacussu	Crotalinae	Sim	Sim	Sim	Sazima, I. (2006). Sazima, I. (1991).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).
Bothrops pulchra	Crotalinae	Sim	Sim	Sim	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).
Bothrops taeniatus	Crotalinae	Sim	Sim	Sim	Martins, M., Marques, O. A., & Sazima, I. (2002). Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Martins, M., Marques, O. A., & Sazima, I. (2002). Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016). https://andrebaertschi.photoshelter.com/gallery-image/Venomous-	Martins, M., Marques, O. A., & Sazima, I. (2002).

						Snakes/G00002f.pbKDVKTQ/I0000uKuwSNyjEGA	
Bothrops chloromelas	Crotalinae		Sim			https://andrebaertschi.photoshelter.com/gallery-image/Venomous-Snakes/G00002f.pbKDVKTQ/I0000MF.Hd1r4gu0 (último acesso em 24/05/19 as 11h02)	
Bothrops bilineatus	Crotalinae	Sim	Sim	Sim	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016). Greene, H. W., & Campbell, J. A. (1972). Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002).	Martins, M., Marques, O. A., & Sazima, I. (2002). https://en.wikipedia.org/wiki/Bothrops_bilineatus

Porthidium dunni	Crotalinae		Sim			https://www.inaturalist.org/observations/2736080 (último acesso em 23/05/19 as 23h24)	
Porthidium ophryomegas	Crotalinae			Sim		.	https://en.wikipedia.org/wiki/Porthidium_ophryomegas (último acesso em 23/05/19)
Porthidium nasutum	Crotalinae	Sim	Sim	Sim	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Lamar, W. W., & Sasa, M. (2003).	J. A. Campbell & W. W. Lamar. (2004).
Porthidium porrasi	Crotalinae		Sim			Lamar, W. W., & Sasa, M. (2003). Solórzano, A. (2004)	.
Porthidium lansbergii	Crotalinae		Sim			Jiménez-Charris, E. *et al.* (2015).	
Porthidium arcosae	Crotalinae	Não	Não	Sim	Valencia, J. H., Vaca-Guerrero, G., & Garzón, K. (2011).	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	Valencia, J. H., Garzón-Tello, K., &

							Barragán-Paladines, M. E. (2016).
Porthidium yucatanicum	Crotalinae		Sim	Sim	J. A. Campbell & W. W. Lamar. (2004).	https://www.inaturalist.org/taxa/31010-Porthidium-yucatanicum (último acesso em 23/05/19 as 23h29)	Castoe, T. A. (2002).
Atropoides picadoi	Crotalinae		Sim			J. A. Campbell & W. W. Lamar. (2004).	.
Cerrophidion petlalcalensis	Crotalinae		Sim	Sim		https://inaturalist.ca/observations/5013643 (último acesso em 23/05/19 as 23h30) J. A. Campbell & W. W. Lamar. (2004).	Jadin, R. C. (2007).
Cerrophidion tzotzilorum	Crotalinae			Sim		J. A. Campbell & W. W. Lamar. (2004).	Jadin, R. C. (2007).
Cerrophidion godmani	Crotalinae		Sim	Sim		J. A. Campbell & W. W. Lamar. (2004). Jadin, R. (2012).	J. A. Campbell & W. W. Lamar. (2004). Solórzano, A. (2004).

Cerrophidion sasai	Crotalinae		Não	Sim		Jadin, R. (2012).	Jadin, R. C. (2007).
Atropoides mexicanus	Crotalinae		Sim	Sim	J. A. Campbell & W. W. Lamar. (2004).	J. A. Campbell & W. W. Lamar. (2004). http://reptile-database.reptarium.cz/species?genus=Atropoides&species=mexicanus	J. A. Campbell & W. W. Lamar. (2004). http://reptile-database.reptarium.cz/species?genus=Atropoides&species=mexicanus http://www.toxinology.com/fusebox.cfm?fuseaction=main.snakes.display&id=SN2627 Solórzano, A. (2004).
Atropoides olmec	Crotalinae		Sim	Sim	J. A. Campbell & W. W. Lamar. (2004).	J. A. Campbell & W. W. Lamar. (2004).	http://www.toxinology.com/fusebox.cfm?fuseaction=main.snakes.display&id=SN03

							66 (último acesso em 24/05/19 as 11h13)
Atropoides nummifer	Crotalinae		Sim	Sim	J. A. Campbell & W. W. Lamar. (2004).	J. A. Campbell & W. W. Lamar. (2004).	Campbell, J. A. (1999).
Atropoides occiduus	Crotalinae		Sim		J. A. Campbell & W. W. Lamar. (2004).	J. A. Campbell & W. W. Lamar. (2004).	J. A. Campbell & W. W. Lamar. (2004).
Ophryacus undulatus	Crotalinae	Não	Não	Sim	Grünwald *et al.,* (2015).	Grünwald *et al.* (2015).	J. A. Campbell & W. W. Lamar. (2004).
Mixcoatlus barbouri	Crotalinae		Sim			J. A. Campbell & W. W. Lamar. (2004).	
Mixcoatlus melanurus	Crotalinae		Sim			J. A. Campbell & W. W. Lamar. (2004).	
Bothriechis schlegelii	Crotalinae	Sim	Sim		Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).	https://www.inaturalist.org/observations/10250810 (último acesso em 15/11/19 as 18h07) Solórzano, A. (2004).	Valencia, J. H., Garzón-Tello, K., & Barragán-Paladines, M. E. (2016).
Bothriechis supraciliaris	Crotalinae		Sim			https://www.inaturalist.org/observations/6318676	

						(último acesso em 24/05/19 as 11h22)	
Bothriechis bicolor	Crotalinae	Sim			Sazima, I. (1991).		
Bothriechis marchi	Crotalinae		Sim			https://www.inaturalist.org/observations/15451945 (último acesso em 24/05/19 as 11h24) McCranie, J. R. (2011).	
Bothriechis thalassinus	Crotalinae		Sim			http://reptile-database.reptarium.cz/species?genus=Bothriechis&species=thalassinus - https://www.inaturalist.org/taxa/30849-Bothriechis-thalassinus/browse_photos ambos acessados por	

						(último em 24/05/19 as 11h31)	
Bothriechis lateralis	Crotalinae	Sim	Sim	Sim	Sazima, I. (1991)	Solórzano, A. (2004). https://en.wikipedia.org/wiki/Bothriechis_lateralis (último acesso em 24/05/19 as 11h41)	Solórzano, A. (2004).
Bothriechis guifarroi	Crotalinae		Sim		Townsend J. H. *et al.* (2013).	Townsend J. H. *et al.* (2013).	
Gloydius ussuriensis	Crotalinae		Sim	Não		Gloyd, H. K., & Conant, R. (1990). https://www.inaturalist.org/observations/18087047 https://www.reptarium.cz/photogallery/vipers/18857 (último acesso em 08/10/19 às 18:16)	Kim, B. S., & Oh, H. S. (2014). Orlov, N. L. *et al.* (2002).

Gloydius brevicaudus	Crotalinae		Sim	Sim		Gumprecht, A. (2004). Gloyd, H. K., & Conant, R. (1990). https://www.biolib.cz/cz/taxonimage/id218592/?taxonid=600939 https://en.wikipedia.org/wiki/Gloydius_brevicaudus https://commons.wikimedia.org/wiki/File:Gloydius_blomhoffi_brevicaudus_(Short-tailed_Mamushi).JPG (último acesso em 09/10/19 às 11h39)	Gao, J. F. *et al.* (2013).
Gloydius blomhoffii	Crotalinae		Sim	Não	Neill, W. T. (1960).	Neill, W. T. (1960). Gloyd, H. K., & Conant, R. (1990).	Mori, A., & Nagata, E. (2016).

Gloydius tsushimaensis	Crotalinae		Sim			Gumprecht, A. (2004).	
Gloydius intermedius	Crotalinae		Sim	Sim		https://www.inaturalist.org/observations/18087048 (último acesso em 09/10/19 as 12h45)	Orlov, N., Ananjeva, N., & Khalikov, R. (2002).
Gloydius halys	Crotalinae		Sim	Sim		Gloyd, H. K., & Conant, R. (1990). https://www.acq.osd.mil/eie/afpmb/docs/lhd/venomous_animals_bycountry.pdf (último acesso em 09/10/19 as 15h45)	Simonov, E. (2009).
Gloydius shedaoensis	Crotalinae	Não		Sim	Shine, R., Sun, L. X., Zhao, E., & Bonnet, X. (2002).		Shine, R., Sun, L. X., Zhao, E., & Bonnet, X. (2002). Shine, R., Sun, L. X., Fitzgerald, M., & Kearney, M. (2002).

							Shine, R., Sun, L., Kearney, M., & Fitzgerald, M. (2002).
Gloydius strauchi	Crotalinae		Não			Gloyd, H. K., & Conant, R. (1990). https://en.wikipedia.org/wiki/Gloydius_strauchi (último acesso em 09/10/19 as 16h46)	
Gloydius liupanensis	Crotalinae			Sim			Gong, D. J. *et al*. (2015).
Trimeresurus gracilis	Crotalinae			Sim			Lin, C. F., & Tu, M. C. (2008).
Ovophis okinavensis	Crotalinae		Sim	Não		Vogel, G. (2006). https://www.flickr.com/photos/cowyeow/27710068818/in/photostream/ (último acesso em 30/10 às 15h41)	Vincent, S. E., & Mori, A. (2007). Mori, A., & Toda, M. (2011). Aird, S. D., *et al.* (2013).

Protobothrops tokarensis	Crotalinae			Sim			Aird, S. D., et al. (2013).
Protobothrops flavoviridis	Crotalinae		Sim	Sim		https://www.flickr.com/photos/okinawaphotos/13284483553/in/photostream/ https://www.inaturalist.org/observations/13012653 https://www.joelsartore.com/ani102-00039/ (último acesso em 30/10/2019 às 15h44)	Aird, S. D., et al. (2013).
Protobothrops elegans	Crotalinae		Sim	Sim		Neill, W.T. (1960).	Aird, S. D., et al. (2013).
Protobothrops maolanensis	Crotalinae			Sim			Aird, S. D., et al. (2013).
Protobothrops dabieshanensis	Crotalinae		Sim	Sim		http://bbs.pxtx.com/thread-958005-1-1.do	Aird, S. D., et al. (2013).

						(último acesso em 30/10/2019 às 15h53)	
Protobothrops xiangchengensis	Crotalinae		Sim	Sim		Vogel, G. (2006). https://www.joelsartore.com/keyword/protobothrops-xiangchengensis/ (Último acesso em 07/08/2019 às 12:16)	Aird, S. D., et al. (2013).
Protobothrops jerdonii	Crotalinae	Sim	Sim	Sim	https://www.reddit.com/r/VenomousKeepers/comments/al0r8c/protobothrops_jerdonii_doing_some_caudal_luring/ (pers. comm.)	Vogel, G. (2006). https://www.reddit.com/r/VenomousKeepers/comments/al0r8c/protobothrops_jerdonii_doing_some_caudal_luring/ (pers. comm.)	Aird, S. D., et al. (2013).
Protobothrops cornutus	Crotalinae		Sim	Sim		https://www.joelsartore.com/ani097-00376/ https://viperbrothers.co.za/galleries/protobothrops-cornutus-gallery/	Aird, S. D., et al. (2013).

						(último acesso em 22/10/3029 às 9:16)	
Protobothrops mangshanensis	Crotalinae	Sim	Sim	Sim	https://www.youtube.com/watch?v=txluLEgmbDg (Último acesso em 02/12/19 às 11:44)	O'Shea, M. (2018).	Aird, S. D., et al. (2013).
Protobothrops sieversorum	Crotalinae			Sim			Aird, S. D., et al. (2013).
Protobothrops kaulbacki	Crotalinae		Sim	Sim		https://indiabiodiversity.org/species/show/275575 (último acesso em 30/10/2019 às 16h10)	Aird, S. D., et al. (2013).
Ovophis tonkinensis	Crotalinae		Sim			Vogel, G. (2006). (pag 74) https://www.hetterrarium.com/en_GB/a-46746560/venomous-reptiles/ovophis-tonkinensis-info-care/	

						https://www.hongkongsnakeid.com/mountain-pit-viper (último acesso em 23/10/19 as 13h24)	
Ovophis monticola	Crotalinae		Sim	Não		Vogel, G. (2006). Gumprecht, A. (2004). Tillack, F., Shah, K. B., Gumprecht, A., & Husain, A. (2003). https://www.inaturalist.org/observations/97669 (último acesso em 23/10/19 as 12h40)	Orlov, N., Ananjeva, N., & Khalikov, R. (2002).
Calloselasma rhodostoma	Crotalinae	Sim	Sim	Sim	Daltry, J. C., Wüster, W., & Thorpe, R. S. (1998). Schuett, Gordon. (1984).	Vogel, G. (2006). Daltry, J. C., Wüster, W., & Thorpe, R. S. (1998). Emmrich, D. (1997). Gumprecht, A. (2004).	http://www.toxinology.com/fusebox.cfm?fuseaction=main.snakes.display&id=SN0080 (último acesso em 22/10/19 as 11h51)

							Daltry, J. C., Wüster, W., & Thorpe, R. S. (1998).
Hypnale nepa	Crotalinae		Sim	Não		https://www.inaturalist.org/observations/31895119 (último acesso em 22/10/19 as 11h30)	Maduwage, K., *et al.* (2009).
Hypnale hypnale	Crotalinae	Sim	Sim		Neill, W. T. (1960). Sawant, N.S., Jadhav, T.D., & Shyama, S.K. (2010). Wharton, C. H. (1960).	Gumprecht, A. (2004). Neill, W. T. (1960). Wharton, C. H. (1960). https://www.inaturalist.org/observations/29100917 (último acesso em 14/10/19 as 11h22)	
Hypnale zara	Crotalinae		Sim			http://www.reptarium.cz/content/photo_rd_09/Hypnale-zara-03000039320_01.jpg (último acesso em 14/10/19 as 10h35)	

Tropidolaemus subannulatus	Crotalinae		Sim			http://www.wildherps.com/species/T.subannulatus.html https://www.ecologyasia.com/verts/snakes/bornean-keeled-pit-viper.htm (último acesso em 14/10/19 as 10h13)	
Tropidolaemus wagleri	Crotalinae		Sim			Neill, W. T. (1960). http://reptile-database.reptarium.cz/species?genus=Tropidolaemus&species=wagleri https://www.ecologyasia.com/verts/snakes/waglers_pit_viper.htm https://www.inaturalist.org/taxa/30936-Tropidolaemus-wagleri/browse_photos	

						(último acesso em 14/10/19 as 09h45)	
Deinagkistrodon acutus	Crotalinae		Sim			Gloyd, H. K., & Conant, R. (1990). https://c8.alamy.com/comp/P96G6C/deinagkistrodon-acutus-hundred-pacer-sharp-nosed-viper-chinese-mocassin-P96G6C.jpg https://www.youtube.com/watch?v=wtQH6ALSMrc https://www.flickr.com/photos/65586506@N04/32426246943 https://animaldiversity.org/accounts/Deinagkistrodon_acutus/ (último	

						acesso em 10/10/19 as 11h25)	
Garthius chaseni	Crotalinae		Sim			https://www.inaturalist.org/observations/12569750 https://www.inaturalist.org/observations/27784928 (último acesso em 09/10/19 as 18h07)	
Azemiops feae	Azemiopinae		Não			https://www.flickr.com/photos/kevinmessenger/7424689830 (último acesso em 09/19/19 as 17h57)	Phelps, T. (2010).
Pareas carinatus	Pareidae	Não	Não	Não	Götz, M. (2002). Gotz, M. (2001).	Gotz, M. (2001).	Götz, M. (2002).
Pareas hamptoni	Pareidae		Sim	Não		Vogel, G. (2010). https://www.flickr.com/photos/rushen/46860945	Götz, M. (2002).

						504/ (último acesso em 30/10/2019 às 22h22)	
Achalinus meiguensis	Xenodermidae			Não			https://www.iucnredlist.org/species/191936/2017823#habitat-ecology (último acesso em 27/11/19 as 18h37)
Achalinus rufescens	Xenodermidae			Não			https://www.iucnredlist.org/species/192099/2039663#habitat-ecology https://www.hongkongsnakeid.com/burrowing-rufous-snake (último acesso em 27/11/19 as 2019)
Acrochordus javanicus	Acrochordidae	Sim	Não	Não	Herping Thailand per. comm.	https://www.youtube.com/watch?v=NVdfWM5Q4ro (último acesso em	https://www.iucnredlist.org/species/176718

					https://www.youtube.com/watch?v=NVdfWM5Q4ro (último acesso em 27/11/2019 às 17h53) Pers. comm.	27/11/2019 às 17h53) pers. comm.	/1443749#habitat-ecology https://animaldiversity.org/accounts/Acrochordus_javanicus/ https://en.wikipedia.org/wiki/Elephant_trunk_snake https://www.youtube.com/watch?v=NVdfWM5Q4ro (último acesso em 27/11/2019 às 18h12)
Acrochordus granulatus	Acrochordidae	Não	Não	Não	https://animaldiversity.org/accounts/Acrochordus_granulatus/ (último acesso em 27/11/19 as 17h19) Voris, H. K., & Glodek, G. S. (2009).	Das, I. (2010). Wangkulangkul, S. (2004).	Das, I. (2010). - Lillywhite, H. B. (1996). Wangkulangkul, S. (2004).

					Wangkulangkul, S. (2004).		
Duberria lutrix	Lamprophiidae	Não	Não	Não	Sazima, I. (1989).	https://bloubergsnakerescue.co.za/our-work/juvenile-common-slug-eater-rescued-near-contermanskloof-20171012/ (último acesso em 03/11/2019 às 17h39) pers. comm.	FitzSimons, V. F. M. (1974).
Liophidium torquatum	Lamprophiidae		Sim			Vieites, D. R., *et al.* (2010).	
Leioheterodon madagascariensis	Lamprophiidae			Não			Mori, A., & Tanaka, K. (2001). https://search.proquest.com/docview/212018474?pq-origsite=gscholar (último acesso em 04/11/2019 às 17h53)

Micrurus surinamensis	Elapidae	Não	Não	Não	Morais, D. H., Ávila, R. W., Kawashita-Ribeiro, R. A., & de Carvalho, M. A. (2011).	https://www.flickr.com/photos/kwray/16715331655 (último acesso em 25/11/19 as 14h53)	Morais, D. H., Ávila, R. W., Kawashita-Ribeiro, R. A., & de Carvalho, M. A. (2011).
Sinomicrurus macclellandi	Elapidae			Não			Das, I. (2010).
Bungarus fasciatus	Elapidae	Não		Não	http://herpingthailand.com/snakes-of-thailand/kraits/bungarus-fasciatus-banded-krait/ (último acesso em 25/11/19 as 12h01)		http://herpingthailand.com/snakes-of-thailand/kraits/bungarus-fasciatus-banded-krait/ (último acesso em 02/12/19 as 09H37) https://en.wikipedia.org/wiki/Banded_krait#cite_note-Knierim,_Tyler_2017-9 https://www.ecologyasia.com/verts/snakes/banded

							_krait.htm (último acesso em 25/11/19 as 12h08)
Ophiophagus hannah	Elapidae	Não	Não	Não	Bhaisare, D., *et al.* (2010).	reptile-database.reptarium.cz/species?genus=Ophiophagus&species=hannah https://www.hongkongsnakeid.com/king-cobra (último acesso em 25/11/19 as 11h06)	Bhaisare, D., *et al.* (2010).
Erpeton tentaculatum	Homolopsidae	Não		Não	Smith, T. L., Povel, G. D. E., & Kardong, K. V. (2006).		https://www.iucnredlist.org/species/176697/7285596#habitat-ecology (último acesso em 24/11/19 as 17h24) Smith, T. L., Povel, G. D. E., & Kardong, K. V. (2006).

Cantoria violacea	Homolopsidae	Não	Não	Não	Jayne, B. C., Voris, H. K., & Ng, P. K. L. (2018).	http://www.andamannicobarsnakes.com/Cantoriaviolacea.html	Fabre, A. C., Bickford, D., Segall, M., & Herrel, A. (2016). http://www.andamannicobarsnakes.com/Cantoriaviolacea.html https://www.iucnredlist.org/species/176678/7282253#habitat-ecology (último acesso em 24/11/19 as 16h40)
Pseudoxenodon bambusicola	Colubridae			Não			Personal communication with HongKong Snake ID authors Adam Francis e Robert Ferguson
Pseudoxenodon karlschmidti	Colubridae			Não			http://www.toxinology.com/fusebox.cfm?f

							useaction=main.snakes.display&id=SN2083 (último acesso em 20/11/19 as 17h38)
Grayia ornata	Colubridae	Não	Não	Não	Pauwels, O. S., Toham, A. K., & Mamonekene, V. (2002).	Chippaux, J. P., & Jackson, K. (2019). http://dkortephoto.com/wordpress/grayia-ornata-ornate-water-snake/ (último acesso em 20/11/19 as 11h27)	Pauwels, O. S., Toham, A. K., & Mamonekene, V. (2002). http://dkortephoto.com/wordpress/grayia-ornata-ornate-water-snake/
Calamaria pavimentata	Colubridae		Não			https://bangkokherps.wordpress.com/snakes/collared-reed-snake/ (último acesso em 13/11/19 as 10h02)	
Sibynophis collaris	Colubridae			Não			https://indiabiodiversity.org/species/show/238778

							http://www.sjonhauser.nl/sibynophis-collaris.html (último acesso em 05/11/19 as 13h35)