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Evolution of vipers and the role of key innovations in their diversification

Evoluce zmijovitých hadů a role klíčových inovací v jejich diverzifikaci

Bachelor´s thesis

Supervisor: Mgr. Jiří Šmíd, Ph.D.

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Podpis

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Abstract

The family Viperidae consists of 36 genera, containing more than 350 species in total. The family is distributed throughout Africa and most of Eurasia, however the greatest diversity is located in North and South America, where more than 40 % of the viper species can be found. The family is thus missing only in Australia, New Guinea, Madagascar, New Zealand and a number of other islands and archipelagos. As with most reptiles, they are also almost completely absent from polar regions, with the exception of *Vipera berus*, the only snake that has ventured north of the Arctic Circle. Their relative evolutionary success is attributed to many so called "key innovations", which include solenoglyphous dentition, viviparity of many genera or heat-sensing pits in the subfamily Crotalinae. Vipers are not only interesting because of their evolutionary history, but they are also subject of important medical studies regarding their venom and toxicity. WHO estimates that around 100,000 people worldwide may die from snake bites each year. This thesis presents a summary of our current knowledge of the evolutionary history of this family, including phylogeny and biogeography, and contemplates the mechanisms behind its amazing diversity.

Keywords

Viperidae, snakes, diversification dynamics, key innovations, phylogeny, evolutionary radiation, biogeography

Abstrakt

Čeleď zmijovitých se skládá z 36 rodů, které společně obsahují přes 350 druhů. Vyskytuje napříč Afrikou a většinou Eurasie, největší druhovou diverzitu ovšem najdeme v Severní a Jižní Americe, kde se vyskytuje přes 40 % všech druhů zmijí. Tato čeleď tedy chybí pouze v Austrálii, na Nové Guineji, Novém Zélandu, Madagaskaru a několika dalších ostrovech a souostrovích. Pochopitelně je také zpravidla nenalezneme ani v polárních oblastech. Výjimkou je zmije obecná (*Vipera berus*), která se jako jediný had vydala i za polární kruh. Relativní evoluční úspěch zmijí se přisuzuje množství „klíčových inovací“, mezi které se řadí třeba solenoglyfní dentice, živorodost, přítomná v mnoha liniích, či termorecepční orgány u zástupců podčeledi Crotalinae. Zmijovití ovšem nejsou zajímaví jen pro svou evoluční historii, jsou také předmětem důležitých medicinálních studií zabývajících se jejich jedy a toxicitou. WHO totiž předpokládá, že více než 100 000 lidí zemře ročně v důsledku uštknutí hady a zmije mají na tomto čísle nezanedbatelný podíl. Tato bakalářská práce představuje shrnutí našeho poznání o evoluční historii této čeledi, včetně fylogeneze a biogeografie, a přemítá o mechanismech zodpovědných za její úžasnou diverzitu.

Klíčová slova

Viperidae, hadi, diverzifikační dynamika, klíčové inovace, fylogeneze, evoluční radiace, biogeografie

Contents

1. Introduction

Vipers are a fascinating lineage of snakes that has attracted and amazed herpetologists and naturalists for centuries. With many recent phylogenetic studies, we are now beginning to understand the evolutionary history of the family. Today, viperids are divided into three subfamilies, Viperinae, Azemiopinae and Crotalinae. These three subfamilies make up a total of 350 species and 36 genera. This makes vipers the third most diverse family among all snakes after Colubridae (*sensu lato*) and Elapidae (Uetz et al., 2022).

The family is characterized by stout bodies and solenoglyphous dentition with long mobile fangs positioned in the front of the jaw. The position of the venom gland gives vipers the signature triangular head shape. Despite the common ancestor being probably oviparous, most of extant viper species are viviparous. This strategy has emerged multiple times independently during the evolution of the family. Viviparity is waged as a potential key innovation that could have sped up the diversification in the group. However, other key innovations have emerged during the evolutionary history of the family and their effect on the diversification dynamics has been studied. These include the unique venom apparatus, thermoreceptive loreal pits or arboreality (Lynch, 2009; Alencar et al., 2016, 2017; Harrington et al., 2018).

The worldwide distribution of vipers also hints at their evolutionary success. The family started radiating in Afro-Arabia or Eurasia. Africa is the main centre of diversity for the subfamily Viperinae and several species-rich genera, such as *Bitis* and *Atheris*, can be found there. However, a substantial part of the diversity of the subfamily, including its most diverse genus, *Vipera*, is found throughout the Western Palearctic and Saharo-Arabia. For crotalines, high diversity is found in South-East Asia, where for instance the genus *Trimeresurus* has diversified into over 50 species. However, the richest radiation of the subfamily has taken place in the Americas; the New World radiation comprises over 40 % of species of the whole family. The vipers have conquered there both North and South America. South America has been colonised multiple times independently, and almost 60 species can be found there, most of them belonging to the genus *Bothrops* (Wüster et al., 2008; Šmíd & Tolley, 2019).

2. Phylogeny of Viperidae

2.1. Fossil Record

The FosFARbase database (fosFARbase, 2021) reports 487 fossils of the Viperidae family members, GBIF (GBIF, 2021) suggests there are 1449 viper fossils. The fossil record comes mainly from vertebrae and fangs, and while the fossil can be sometimes assigned to a certain clade, it is often difficult to identify them at generic or species level (Šmíd & Tolley, 2019).

The first known fossils come from the very early Miocene (ca. 22 Ma) from Western Europe and are assigned to species *Provipera boettgeri*, *Vipera antiqua* and "*Vipera* sp." (Szyndlar & Rage, 2002; Kuch et al., 2006; Šmíd & Tolley, 2019; fosFARbase, 2021), However, the first diversification processes in the family are estimated to have begun between 60 and 30 Ma and it is unclear whether the aforementioned fossils can be assigned to *Vipera*, considering the fact that recent species of the genus did not start to diversify until 15 – 12 Ma (Wüster et al., 2008; Lynch, 2009; Alencar et al., 2016; Šmíd & Tolley, 2019; Zaher et al., 2019).

Interesting records also come from Africa, an approximately 17Ma old "*Bitis* sp." fossil was found in Namibia together with another viperid, morphologically reminiscent of the genus *Vipera* or *Daboia*. Another lower Miocene fossil, *Vipera maghrebiana*, was found in Beni Mellal, Morocco, and based on the morphology it seems to be related to *Vipera aspis*. Pliocene and lower Pleistocene records from Africa include the first occurrence of the genus *Cerastes* and a discovery of a species named *Bitis olduvalensis*, both from Tanzania. Finally, there is a late Pleistocene fossil from Egypt tentatively assigned to the genus *Causus* (Rage, 1976, 2003; Szyndlar & Rage, 2002; Rage & Bailon, 2011; Šmíd & Tolley, 2019).

Regarding the subfamily Crotalinae, the oldest record comes from lower Miocene from Nebraska (Holman, 1981), however, all recent molecular studies (e.g.: Wüster et al., 2008; Alencar et al., 2016) show that the initial radiation of crotalines occurred in the Old World. There, "Crotalinae gen. et sp. indet. A" and "Crotalinae gen. et sp. indet. B" were found in Ukraine in fossiliferous layers approximately 11 My old (Ivanov, 1999). Another Old-World record comes from Japan from the Burdigalian stage of the early Miocene and the fossil has been identified as cf. *Trimeresurus* (Holman & Tanimoto, 2004). Biogeographical interest also concerns fossils from South America. While most of the fossils in the continent are of a Pleistocene origin, the earliest records, belonging to the genus *Bothrops*, come from the late Miocene (Albino, 1995; Albino & Montalvo, 2006; Albino & Brizuela, 2014).

2.2. Phylogenetic Position of Viperidae

The family Viperidae is a member of the class Reptilia, order Squamata and suborder Serpentes. The family belongs into a clade of snakes called Caenophidia. Within this group, viperids are then widely agreed to be positioned as a sister group to a clade consisting of families Homalopsidae, Elapidae, Lamprophiidae, Colubridae and several *incertae sedis* taxa, and with many authors dividing Lamprophiidae and Colubridae into multiple families (Pyron et al., 2013; Zheng & Wiens, 2016; Zaher et al., 2019; Burbrink et al., 2020). As an alternative, one study places Viperidae as a sister family to Pareatidae, although with low support (Figueroa et al., 2016).

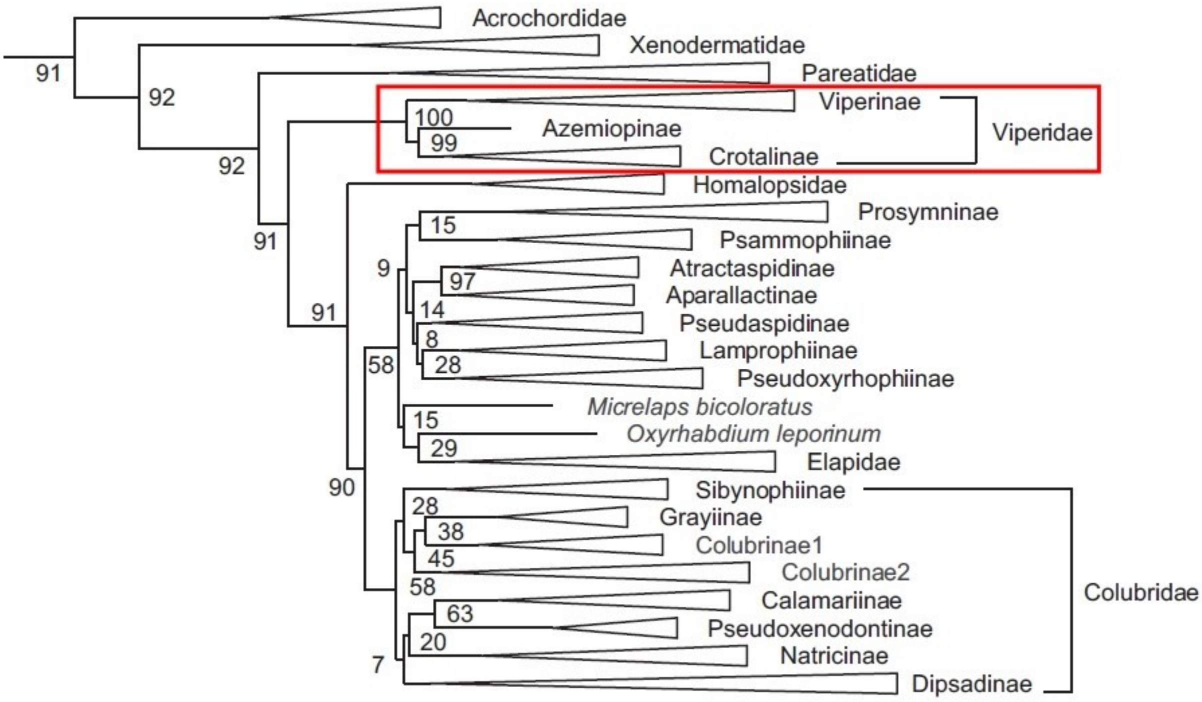

Fig. 1 – Molecular phylogeny of the clade Caenophidia. Taken from Zheng & Wiens (2016). Position of Viperidae highlighted.

2.3. Phylogenetic Relationships amongst Subfamilies

Viperidae are traditionally divided into three subfamilies: Viperinae, Azemiopinae and Crotalinae. While both Viperinae and Crotalinae are relatively species-rich taxa, the subfamily Azemiopinae comprises only one genus, *Azemiops*, with two species, *A. feae* and *A. kharini*. Several authors have proposed, mainly before the era of molecular phylogenies, also a fourth subfamily for the genus *Causus* for their several distinct morphological features, such as prolonged venom glands and a round pupil (Mallow et al., 2003). *Causus*, with their seven species, are now ranked under Viperinae. However, many molecular studies consider them a basal lineage of this subfamily (Šmíd & Tolley, 2019; Zaher et al., 2019), in one case together with the genus *Proatheris* (Figueroa et al., 2016), while others put them either close to *Echis* and/or *Cerastes* (Wüster et al., 2008; Lynch, 2009; Fenwick et al., 2012; Pyron et al., 2013) or into the “Subsaharan clade” with *Bitis*, *Atheris* and *Proatheris* (Pook et al., 2009; Alencar et al., 2016).

Regarding the currently recognized subfamilies, almost all recent molecular studies (Fig. 2) position Viperinae as sister to Azemiopinae and Crotalinae, those two thus make one monophyletic clade, that has probably diverged about 40 Ma (Wüster et al., 2008; Alencar et al., 2016). However, phylogeny based on morphology reconstructs the genera *Causus* and *Azemiops* in basal positions of the phylogenetic tree (Fig. 3) (Hsiang et al., 2015).

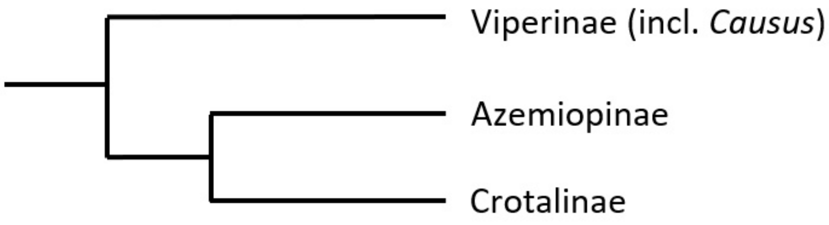

Fig. 2 – Phylogeny of viperid subfamilies based on molecular data (Wüster et al., 2008; Lynch, 2009; Pook et al., 2009; Fenwick et al., 2012; Pyron et al., 2013; Hsiang et al., 2015; Alencar et al., 2016; Figueroa et al., 2016; Zheng & Wiens, 2016; Šmíd & Tolley, 2019; Zaher et al., 2019)

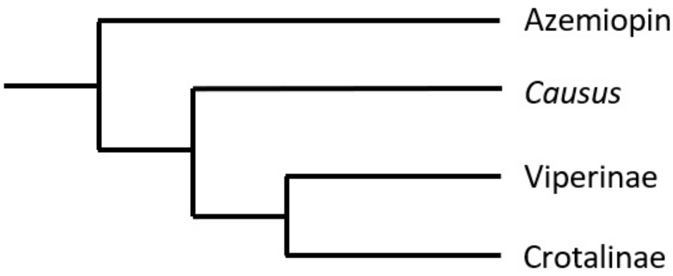

Fig. 3 – Phylogeny of viperid subfamilies based on morphology (Hsiang et al., 2015)

2.4. Phylogeny of Viperinae

Th subfamily Viperinae consists of about 105 species in 13 genera. While different studies disagree on their exact phylogenetic positions and relationships, we are roughly able to divide the subfamily into three biogeographically distinct clades: Subsaharan, Saharan and Palearctic (Wüster et al., 2008; Lynch, 2009; Pook et al., 2009; Alencar et al., 2016; Šmíd & Tolley, 2019; Zaher et al., 2019; Uetz et al., 2022).

Fig. 4 – Examples of Viperinae. Left: *Echis coloratus*; Right: *Vipera ammodytes*. Both pictures original.

2.4.1. Subsaharan Clade

The Subsaharan clade includes genera *Bitis*, *Atheris*, *Proatheris* and, in some studies, *Causus*. The uncertainty about the position of this genus has been addressed earlier. Most studies put *Proatheris* as sister to *Bitis* and *Atheris* (Lynch, 2009; Fenwick et al., 2012; Šmíd & Tolley, 2019; Zaher et al., 2019), some however consider *Bitis* as the basal genus of the clade (Alencar et al., 2016) or even as the basal genus of the whole subfamily Viperinae (Pook et al., 2009). Some authors also assign *Proatheris* to a different clade (Pyron et al., 2013; Figueroa et al., 2016). The monotypic genus *Montatheris* may also be a member of the Subsaharan clade based on its distribution but it has not been included in any molecular studies (Alencar et al., 2018).

The genus *Bitis* currently includes 18 species (Uetz et al., 2022). The centre of its diversity is located in southern Africa, with several species inhabiting rainforests and mountains of central Africa. The genus is traditionally divided into four subgenera, each considered monophyletic. The subgenera *Bitis* and *Kenyabitis* are monotypic, with one of them being sister to the rest of the genus, yet it is not clear which one it is. The other two subgenera, *Macrocerastes* and *Calechidna* seem to be two sister lineages (Wittenberg et al., 2015; Gower et al., 2016; Barlow et al., 2019; Ceríaco et al., 2020).

Atheris is represented by 18 species inhabiting rainforests of Subsaharan Africa (Uetz et al., 2022). Most of them are arboreal, which is an exception in the subfamily Viperinae. The phylogenetic relationships in this genus have been explored only briefly, with Menegon et al. 's study being the only recent analysis focused solely on this genus. The study included 10 species and uncovered several radiations within the genus (Menegon et al., 2014).

Proatheris and *Montatheris* are both monotypic genera, both formerly considered as members of the genus *Atheris*. *Proatheris superciliaris* is a rather small viper inhabiting wet savanna on northern and southern shores of Lake Malawi. *Montatheris hindii* is also a small species, endemic to high altitudes of Kenyan Aberdare Mountains and Mount Kenya (Phelps, 2010).

2.4.2. Saharan Clade

The Saharan clade consists of two genera, *Cerastes* and *Echis*, in some studies also joined by *Causus* (Wüster et al., 2008; Lynch, 2009; Fenwick et al., 2012; Pyron et al., 2013). The study of Fenwick et al. also proposes *Echis* as a sister lineage to the rest of Viperinae, however this result together with the dating of the tree raise some questions about the methodology of the study (Fenwick et al., 2012).

The genus *Cerastes* is found in deserts of northern Africa and the Middle East, and it includes four species. However one of the species, *C. boehmei*, is known only from one museum specimen collected in Tunisia with no genetic data available. Other specimens have been destroyed (Wagner & Wilms, 2010).

Twelve species are currently recognized in the genus *Echis*, more advanced phylogenetic methods and more thorough sampling may reveal more. Four species groups are traditionally recognized, with the "*ocellatus* group" being sister to the "*carinatus* group", and the "*pyramidum* group" being sister to the "*coloratus* group" (Barlow et al., 2009; Pook et al., 2009).

2.4.3. Palaearctic Clade

The Palearctic clade of Viperinae includes six genera, which can be further divided into three monophyletic groups, each of two genera.

The first group includes the monotypic genus *Eristicophis* with a sole species *E. macmahonii* found in arid areas of Baluchistan. The other genus from this group, *Pseudocerastes*, consists of three species distributed throughout the deserts of the Middle East (Fathinia et al., 2018).

The second group consists of genera *Montivipera* and *Macrovipera*. *Macrovipera* comprises two to three species, the genus *Montivipera* includes eight, divisible into two complexes, *xanthina*-complex and *raddei*-complex (Stümpel et al., 2016). From a perspective of a Czech zoologist, it may be interesting that the genus *Macrovipera* was distributed in Central Europe in the past, during the late Miocene, as fossils of an extinct species *Macrovipera gedulyi* have been found in Hungary (Szyndlar & Rage, 2002; Šmíd & Tolley, 2019).

The third group consists of the most species-rich genus of all Viperinae, *Vipera*, and its close relatives in the genus *Daboia*. *Vipera* includes 20 to 26 species, with some like *V. walser*, *V. transcaucasiana* or *V. monticola* not always considered valid (Velo-Antón et al., 2012; Ghielmi et al., 2016; Mulder, 2017; Freitas et al., 2020; Speybroeck et al., 2020; Martínez-Freiría et al., 2021; Uetz et al., 2022). The genus is distributed throughout Europe and all the way to eastern Russia and the Korean peninsula. Its distribution area also makes it the only genus of vipers present in central Europe and the Czech Republic. As the disagreements about the validity of several species may suggest, the systematics of the genus is still very much a work in progress, with particularly the *ursinii-renardii* complex seeming to be quite complicated to resolve (Gvoždík et al., 2012; Ghielmi et al., 2016; Mizsei et al., 2017) and possible mtDNA introgressions between different species groups, as may be the case of *Vipera walser* (Ghielmi et al., 2016; Speybroeck et al., 2020; Doniol-Valcroze et al., 2021). The genus *Daboia* contains four species (Freitas et al., 2020; Uetz et al., 2022).

2.5. Phylogeny of Crotalinae

The subfamily Crotalinae consists of 21 genera and approximately 250 species. Several studies divided the subfamily into four monophyletic groups, three Asian clades and the New World radiation (Fenwick et al., 2012; Alencar et al., 2016). But while this solution seems to be quite an elegant one, many questions are still to be answered, not only whether it correctly reflects the evolutionary history of the subfamily but also addressing the seeming paraphyly or polyphyly of several genera, including *Trimeresurus*, *Ovophis* and *Bothrops* (Malhotra & Thorpe, 2004; Fenwick et al., 2012; Alencar et al., 2016; Šmíd & Tolley, 2019). Nevertheless, for the purpose of this thesis, I will be following the proposed four-group division.

Fig. 5 – Examples of Crotalinae. Left: *Bothriechis schlegelii*; Right: *Lachesis stenophrys*. Both pictures original.

2.5.1. Asian Clades

The three Asian clades cannot really be named based on morphology or biogeography. The first and the most basal, includes the genera *Calloselasma*, *Deinagkistrodon*, *Garthius*, *Hypnale* and *Tropidolaemus*, with the first three genera each being monotypic. The genus *Hypnale* consists of three species; five species are recognized in the genus *Tropidolaemus*. Regarding the phylogenetic relationships between these genera, most authors agree that *Hypnale* is close to *Calloselasma* but some place this two-genera group as the most basal lineage of all Crotalinae (Castoe & Parkinson, 2006; Wüster et al., 2008; Figueroa et al., 2016).

The second clade consists solely of the genus *Trimeresurus* (Fenwick et al., 2012; Alencar et al., 2016; Figueroa et al., 2016; Zaher et al., 2019). However, with over 50 species and several new ones described just in last few years, *Trimeresurus* may very well be the most species-rich genus in all Viperidae. Some authors have attempted to divide *Trimeresurus* into multiple genera, but these were all recently downgraded to a subgeneric level (Malhotra & Thorpe, 2004; David et al., 2011; Guo & Wang, 2011). Malhotra & Thorpe (2004) identify several species groups within the genus but with several species described in recent years, a new inquiry into the genus using advanced phylogenomic methods is needed for us to properly understand its evolutionary history. However, what many studies agree upon is the polyphyly of the genus, since *Trimeresurus gracilis* seems to belong to a different clade with *Ovophis okinavensis* as its closest relative (Malhotra & Thorpe, 2004; Wüster et al., 2008; Fenwick et al., 2012; Alencar et al., 2016; Šmíd & Tolley, 2019).

The third clade includes the genera *Gloydius*, *Ovophis* and *Protobothrops*. The genus *Ovophis* is sister to *Protobothrops*, while *Gloydius* seems to be the closest to a clade comprising *Trimeresurus gracilis* and *Ovophis okinavensis*. This renders both, *Ovophis* and *Trimeresurus*, polyphyletic. Šmíd & Tolley (2019) also inferred the rest of *Trimeresurus* into the clade. *Gloydius*, the only genus of crotalines reaching the Western Palearctic, features over 20 species with several new ones described in the last few years (Wagner et al., 2016; Shi et al., 2018). The evolutionary history of the genus seems to be complicated, as several species appear to be polyphyletic, and some subspecies were recently elevated to a species level. Three main groups can be recognized within the genus – the *blomhoffii* complex, the *strauchi* complex and the *intermedius-halys* complex (Yan et al., 2012; Rastegar-Pouyani et al., 2018; Asadi et al., 2019; Shi et al., 2021). The genus *Protobothrops* includes 15 species, with some formerly belonging to other genera that had been synonymized with *Protobothrops*. Guo et al. identify three species groups within the genus (Guo et al., 2016).

2.5.2. New World Radiation

The New World radiation includes over 150 species, thus making up for more than 40 % of the species diversity in the whole family (Alencar et al., 2018). As with many rapid evolutionary radiations, the process of the New World radiation of vipers is difficult to reconstruct. However, several studies have found four main clades (Fig. 6) within the radiation (Pyron et al., 2013; Figueroa et al., 2016; Zaher et al., 2019), while multiple other studies show smaller or larger deviations from this system (Castoe & Parkinson, 2006; Lynch, 2009; Pook et al., 2009; Jadin et al., 2011; Fenwick et al., 2012; Alencar et al., 2016; Šmíd & Tolley, 2019). Recent study has found an interestingly intensive degree of gene flow and molecular introgression in the early diversification of the genus *Crotalus* (specifically the "Western rattlesnake species group") (Myers, 2021). It can be presumed that similar processes may have driven diversification of the whole New World Radiation (and other radiations in the family), as hybridisation and introgression can play a crucial role in such evolutionary events (Meier et al., 2017).

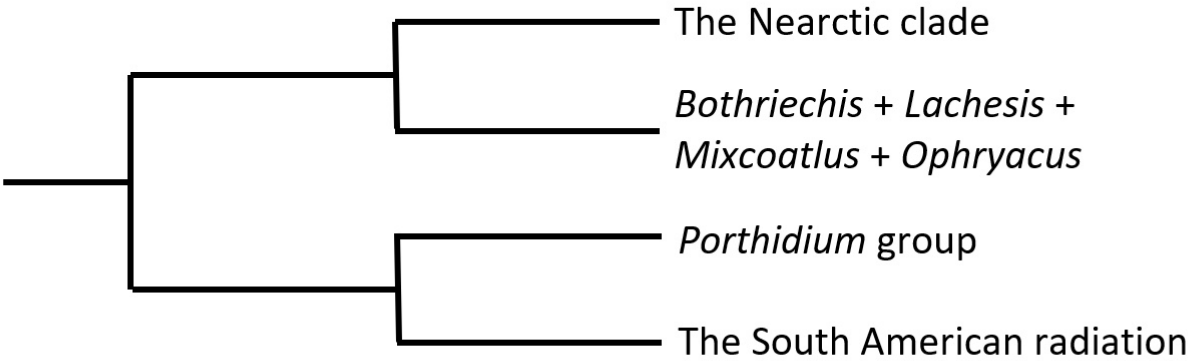

Fig. 6 – Phylogeny of the New World radiation according to Pyron et al. (2013), Figueroa et al. (2016), Zaher et al. (2019).

The first of these clades ("The Nearctic clade"), also considered basal in the whole radiation by some (Castoe & Parkinson, 2006; Fenwick et al., 2012; Šmíd & Tolley, 2019), consists of genera *Agkistrodon*, *Sistrurus* and *Crotalus*. While some studies exclude *Agkistrodon* from the clade (Castoe & Parkinson, 2006; Fenwick et al., 2012; Šmíd & Tolley, 2019), most authors agree upon the monophyly of the clade, especially regarding the close relationship of *Crotalus* and *Sistrurus* based not only on molecular data but also due to the presence of the rattle, structure considered to be unlikely to evolve twice independently within the same radiation (Alencar et al., 2018). Of these three genera, *Sistrurus* is the least diverse with two species generally accepted as valid. The genus *Agkistrodon* traditionally included three species with several subspecies. However, several of the subspecies have been later elevated to a species status, raising the diversity up to six to eight (Uetz et al., 2022). Yet the clades formed within the phylogeny of the genus still correspond with the three "original" species, with the *contortrix* species group being sister to the rest of the genus (Parkinson et al., 2000; Alencar et al., 2016; Zaher et al., 2019). The genus *Crotalus* consists of more than 50 species, with several new ones described just recently. However, the delimitation of some species is questionable (Blair & Sánchez-Ramírez, 2016; Alencar et al., 2018; Carbajal-Márquez et al., 2020; Velasco et al., 2022).

The second clade within the radiation includes the genera *Bothriechis*, *Lachesis*, *Mixcoatlus* and *Ophryacus*. However, Alencar et al. (2016) reconstructed the genus *Lachesis* as basal in the New World radiation. Although the statistical support for this relationship was weak in the study, it is worth examining considering that *Lachesis* is the only oviparous genus in the radiation (Fenwick et al., 2012; Alencar et al., 2016, 2018). This genus whose members are the longest vipers in the world consists of four species (Barrio-Amoros et al., 2020; Diniz-Sousa et al., 2020). The position of the genus *Bothriechis* encompassing eleven species is also a subject of discussions as it is often positioned closer to the *Porthidium* group and the South American radiation (Castoe & Parkinson, 2006; Lynch, 2009; Jadin et al., 2011; Alencar et al., 2016). The genera *Ophryacus* and *Mixcoatlus* are both endemic to Mexico and each have three species. Their close phylogenetic relationship is well supported (Jadin et al., 2011; Alencar et al., 2016).

The *Porthidium* group contains four genera: *Porthidium*, *Atropoides*, *Cerrophidion* and *Metlapilcoatlus*. The monophyly of this group is well established, but the inner phylogeny of the clade is yet to be resolved. The genus *Metlapilcoatlus* was erected after increasing support for the paraphyly of *Atropoides* (now monotypic with *A. picadoi* as the sole species). There are six species in the genus *Metlapilcoatlus*, with *M. borealis* described only in 2021 (Campbell et al., 2019; Tepos-Ramírez et al., 2021). The genus *Porthidium* consists of nine species.

The South American radiation includes the genera *Bothrops* (45 species) and *Bothrocophias* (7). However, recent studies show potential polyphyly within both genera as *Bothrops lojanus* seems to be a member of the genus *Bothrocophias*, whereas *Bothrocophias campbelli* could be phylogenetically closer to *Bothrops* (Alencar et al., 2016; Figueroa et al., 2016; Šmíd & Tolley, 2019; Zaher et al., 2019).

3. Evolution of Life History Traits and Key Innovations

The relative evolutionary success of the family Viperidae is credited to a number of so called "key innovations", newly emerged traits which are opening doors to evolutionary radiations. However, the identification of such innovations can be quite difficult as provably testing whether the radiation is a direct result of a specific innovation usually requires multiple convergent developments of such a trait (Heard & Hauser, 1995; Alencar et al., 2016).

3.1. Venom Apparatus

All members of the family have solenoglyphous dentition (Fig. 7), meaning the fangs are positioned in the front and are capable of movement. The venom gland is usually short and located in the back of the head, giving it the signature triangular shape. This type of dentition is unique to viperids, however, quite similar dentition has convergently evolved in the genus *Atractaspis* (family Atractaspididae), where the snake is capable of envenomation even with its mouth closed (Kochva, 1987; Alencar et al., 2018).

The venom apparatus is relatively similar within the whole family, yet dissimilarities can be found in some genera. The fangs in the genus *Causus* are shorter and the venom gland is considerably prolonged along the back making the head narrower than in other vipers. This gives these snakes, together with a round pupil, a more "colubrid-like" appearance (Mallow et al., 2003). Another distinction can be found in the genus *Azemiops*, the sole taxon in the subfamily Azemiopinae. The fangs are also shorter than in the rest of viperids and they carry specific structures not seen in other members of the family: "*a ridge at the tip lateral to the discharge orifice, and a bladelike structure on the ventral surface*." (Mebs et al., 1994; Mallow et al., 2003)

The venoms have mostly proteolytic components, however in some species, such as *Bitis atropos*, neurotoxins can be prevalent (Lee et al., 1982). It is important to note that the composition of the venom can differ not only among different populations of the same species, as could be demonstrated in the case of *Vipera berus*, but also during the ontogeny of a single individual (Mallow et al., 2003; Damm et al., 2021).

It is presumed that the evolution of venom apparatus has allowed the vipers to live with a lower metabolism rate. Compared to some other snakes, their sit-and-wait predation strategy enabled by the presence of the venom apparatus is energetically cheaper than active hunting relying on constriction. This could be a partial explanation of their relative evolutionary success in unfavourable environments, where low energy expenses are necessary, such as deserts or high altitudes (Savitzkyi, 1980; Alencar et al., 2018).

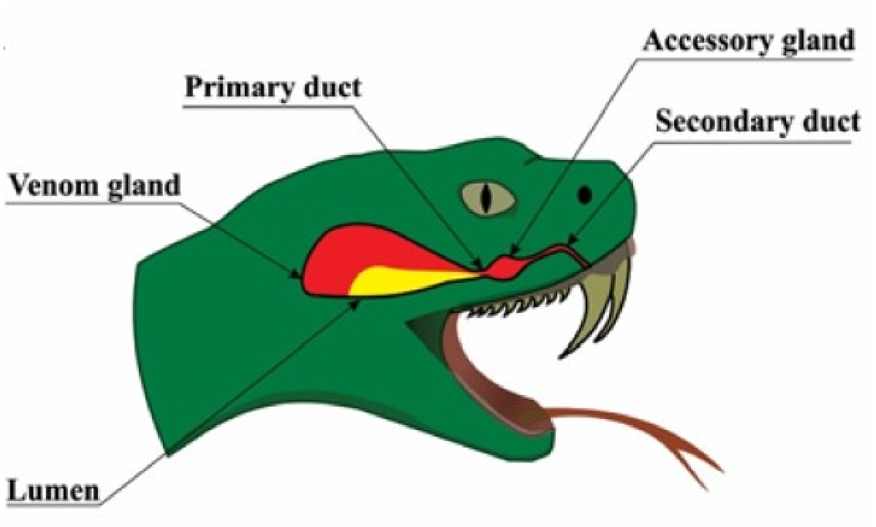

Fig. 7 – Venom apparatus of vipers. Taken from Pucca et al. (2020)

3.2. Evolution of Viviparity

Though the common ancestor of all vipers is considered to be oviparous (Lynch, 2009; Fenwick et al., 2012), viviparity is found at least in 25 of the extant genera, compared to 15 oviparous. However, in some genera, both reproductive modes are present. Viviparity is considered to have evolved multiple (at least 13) times independently in the family, though some lineages have seen a return to oviparity, thus potentially breaking the Dollo’s law of irreversibility (Dollo, 1893; Lynch, 2009; Fenwick et al., 2012).

Viviparity is another key innovation considered important for the diversification of vipers, as the diversification rate has been found higher in live-bearing lineages (Lynch, 2009). This feature is commonly considered as an adaptation to colder climate, as the incubation temperature is more stable (Shine, 2004). It has thus helped the viperid snakes to better cope with colder climates, allowing them to survive in higher altitudes and latitudes and during globally cooler periods, especially the cooling during the Oligocene when the Antarctic ice sheets were established (O’Brien et al., 2020). This is an epoch considered essential for the early diversification of the family and a difference in the pace of diversification of oviparous and viviparous lineages during Oligocene can be seen (Fig. 8) (Lynch, 2009). Aside from low temperatures, it has also been suggested that viviparity can serve as an adaptation to hypoxia in high altitudes (Watson & Cox, 2021). Higher diversification rates among viviparous lineages contrasted to oviparous ones have been found also in other vertebrates, such as fish from the order Cyprinodontiformes (Helmstetter et al., 2016).

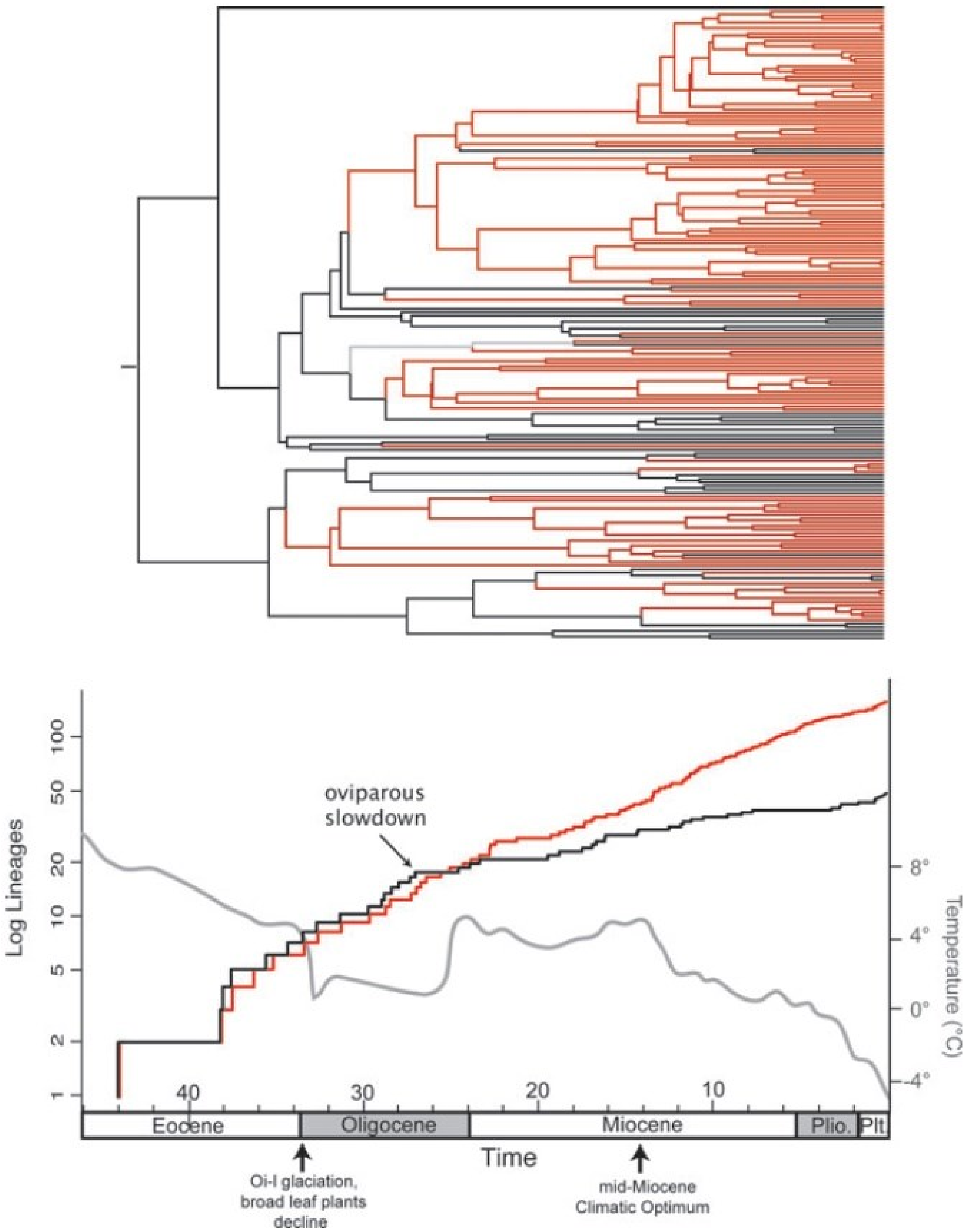

Fig. 8 – Visualization of the difference in the pace of diversification rates in oviparous and viviparous lineages of vipers since the Oligocene. Viviparous lineages are in red, oviparous in black. Taken from Lynch (2009).

From a phylogenetic point of view, egg-laying is present in both lineages traditionally branded as "primitive", the genera *Causus* and *Azemiops*. This is, however, no guarantee of a basal position in a phylogenetic tree. In the subfamily Viperinae, oviparity is relatively more common than in crotalines, occurring in more than half of the genera. *Causus*, *Eristicophis*, *Pseudocerastes* and *Macrovipera* are considered solely oviparous, while in *Echis* and *Cerastes*, oviparity is the dominant strategy. In the species of the genus *Daboia*, the two reproductive modes are equally represented. The remaining genera are then considered viviparous. Despite our lack of knowledge of the ecology and phylogenetic position, viviparity is also presumed in the genus *Montatheris*, given the montane habitat and the high altitude of its distribution range. In the Asian lineages of crotalines, *Calloselasma*, *Deinagkistrodon* and *Ovophis* are considered strictly egg-laying. Oviparity also occurs in some species of *Protobothrops* and *Trimeresurus*. Regarding the New World vipers, the whole radiation appears to be viviparous with the exception of the genus *Lachesis* (Lynch, 2009; Fenwick et al., 2012).

3.3. Thermoreception

Thermoreceptive "pits" has appeared several times independently during the evolution of snakes, and are found in families Boidae, Pythonidae and Viperidae. Within viperids, the heat-sensing loreal pits can be considered an apomorphy of the subfamily Crotalinae (Fig. 9). This adaptation helps the snakes to track their prey after envenomation and to potentially avoid predators (Hartline, 1974; Alencar et al., 2018). The thermoreceptors are waged as another potential key innovation, as the subfamily is the most diversified amongst viperids, though the hypothesis has not been directly tested (Alencar et al., 2016).

Fig. 9 – Position of the thermoreceptive organ in *Bothrops asper*. Original picture.

3.4. Arboreality

This ecological strategy was long thought of as another potential booster for the diversity of the family, though recent studies agree that arboreality does not affect species diversification in vipers (Alencar et al., 2017; Harrington et al., 2018; Tingle & Garland, 2021). It does however put a strong limit on morphological evolution, as arboreal species of vipers typically have a constrained body length and are slenderer compared to terrestrial species. They also tend to have relatively longer, prehensile tails that can be used as anchors (Alencar et al., 2017; Harrington et al., 2018).

About 27 % of all viper species are considered primarily arboreal or at least semi-arboreal. Though vipers are thought to have had a terrestrial common ancestor, arboreality has evolved in multiple lineages during the evolution of the family, probably seven to nine times (Alencar et al., 2018; Harrington et al., 2018). The primarily arboreal vipers are almost exclusively found in tropical and subtropical rain and cloud forests. This includes the genus *Atheris* from the subfamily Viperinae, found in rainforests of Africa. In the subfamily Crotalinae, arboreal genera *Protobothrops*, *Trimeresurus* and *Tropidolaemus* inhabit forests of South-eastern and Eastern Asia, while representatives of the genera *Bothriechis*, *Ophryacus* and some species of

Bothrops live in the trees and bushes of the rainforests of Central and South America (Alencar et al., 2018; Harrington et al., 2018). The semi-arboreal vipers, however, can be found in much more arid habitats. A typical example of such species is *Macrovipera schweizeri* from the island of Milos in the Mediterranean sea, which uses its ability to climb trees to hunt sleeping birds or fledgelings (Andrén et al., 1999; Harrington et al., 2018). In some lineages, the phenomenon of secondary terrestriality can be found. Species falling under this category are *Atheris barbouri* (formerly considered a sole member of the monotypic genus *Adenorhinos*) and *Trimeresurus strigatus* (Mallow et al., 2003; Phelps, 2010; Menegon et al., 2014; Harrington et al., 2018).

3.5. Sidewinding

Sidewinding is a type of locomotion typical for desert snakes, in which the animal tries to minimize the contact of its body with the scorching ground beneath. It is faster than the common ways of snake locomotion, especially on smooth surfaces. The process is depicted on the picture below (Fig. 10), the main point is that the snake touches the surface only with two sections of its body at a time (Klauber, 1956; Tingle & Garland, 2021). Sidewinding can be found in six genera of vipers, five of them belong to the subfamily Viperinae (*Bitis*, *Cerastes*, *Echis*, *Eristicophis*, *Pseudocerastes*). In crotalines, *Crotalus cerastes* is the only species using this type locomotion (Tingle & Garland, 2021).

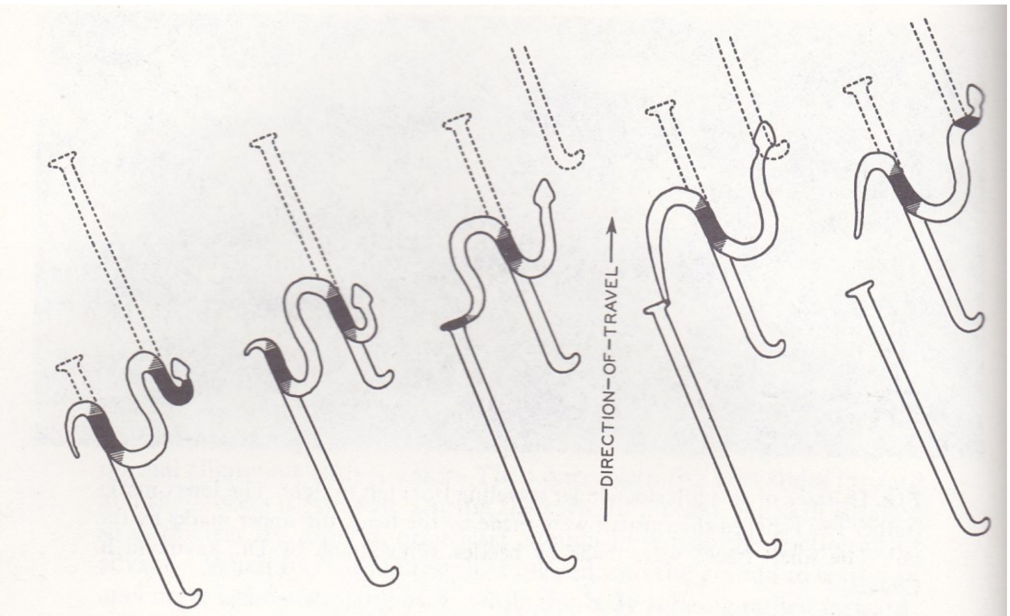

Fig. 10 – Schematic depiction of the process of sidewinding. Taken from Klauber (1956).

3.6. Feeding Ecology

Viperid snakes feed on a wide array of animals, ranging from small rodents as the most common food source to some of the more unusual specialists, such as *Bothrops alcatraz*, feeding mainly on centipedes (Marques et al., 2002; Alencar et al., 2018). Some species, such as *Proatheris superciliaris* or species in the genus *Causus*, feed mostly on frogs (Mallow et al., 2003). *Agkistrodon piscivorus* is considered the only truly semiaquatic species of the family, as it is primarily fish-eating (Gloyd & Conant, 1990). However, despite the existence of several specialized species, most vipers can be considered generalist predators, feeding on small mammals, lizards, birds and amphibians (Alencar et al., 2018).

3.6.1. Caudal Luring and Other Tail Modifications

To attract their prey as the typical sit-and-wait predators, many species use a technique called caudal luring. Especially in younger animals, the tail tip has a light and bright colouration to attract potential prey items that might mistake it for a worm (Heatwole & Davison, 1976; Alencar et al., 2018). Perhaps the most elaborate case of caudal luring has evolved in the species *Pseudocerastes urarachnoides*, whose tail-tip resembles an arachnid. Together with a cryptical colouration pattern, this makes the species a very efficient hunter in deserts of western Iran, where feeding opportunities are scarce and usually consist of migrating birds appearing in the area only twice a year (Fathinia et al., 2009).

In the genera *Crotalus* and *Sistrurus*, the structure known as rattle has evolved. The rattle, while vibrating, can produce a loud sound designed to scare away predators or large herbivores. The structure is unique among all reptiles, however, the usage of tail vibrating against leaves is an antipredatory mechanism known amongst many snake families. Some island species and subspecies of the genus *Crotalus* have lost the rattle, probably due to the absence of selection pressures. These include *C. catalinensis*, *C. lorenzoensis* or *C. estebanensis* (Klauber, 1956).

3.7. Karyotype Evolution

There is not much variability in the known karyotypes of the viperid snakes. Almost all of them, representing both major subfamilies, have 18 chromosome pairs, with 16 macrochromosomes and 20 microchromosomes. The only known exception is *Vipera aspis* with 21 chromosomal pairs (22 macrochromosomes, 20 microchromosomes). However, the variability can be wider in reality, as the karyotypes of the more phylogenetically “interesting” genera such as *Causus* or *Azemiops* have probably not been studied (Singh, 1972; Yosida & Toriba, 1986).

4. Biogeography

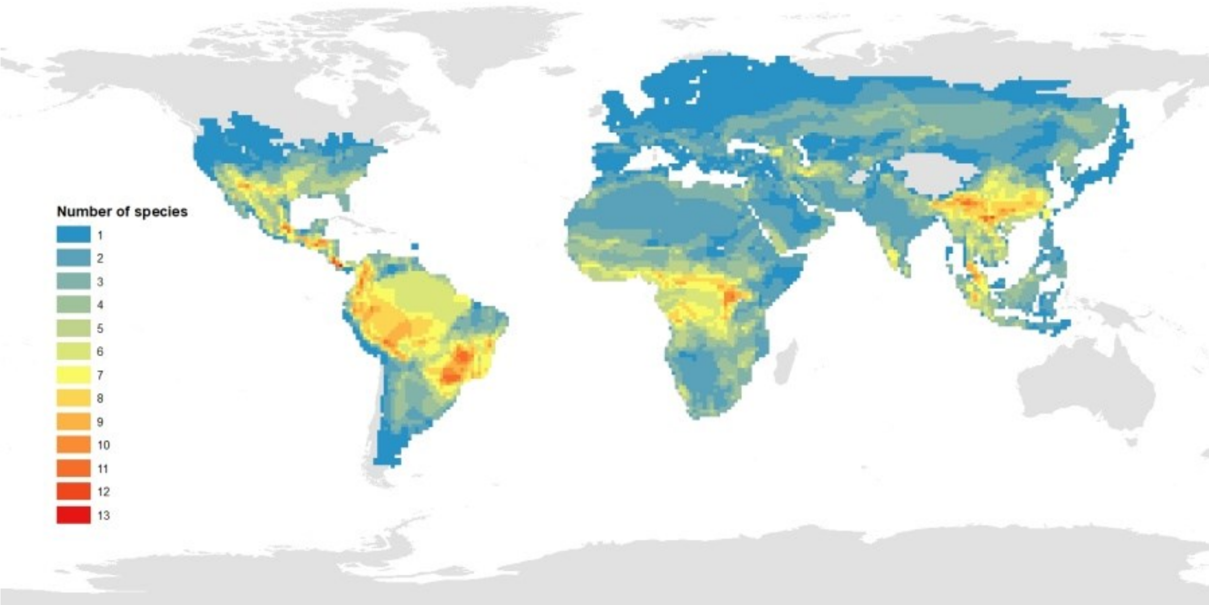

Fig. 11 - Species richness of viperid snakes around the world. Picture original, made by J. Šmíd & V. Waldhauser, using RStudio and ArcGIS, data from Roll et al. (2021).

4.1. Biogeographical Origins of Viperidae

Viperid snakes are distributed almost throughout the whole world, missing, apart from polar regions, only in the Madagascan, Australian and Oceanian zoogeographical realms (Holt et al., 2013; Šmíd & Tolley, 2019; Roll et al., 2021). The family has started to diversify during the early Paleogene, with studies putting the estimate between 60 to 30 Ma, however, the earliest fossils come from 22 Ma (Szyndlar & Rage, 2002; Kuch et al., 2006; Wüster et al., 2008; Lynch, 2009; Alencar et al., 2016; Šmíd & Tolley, 2019; Zaher et al., 2019). The initial radiation of the family is placed either into Eurasia or Afro-Arabia (Wüster et al., 2008; Šmíd & Tolley, 2019).

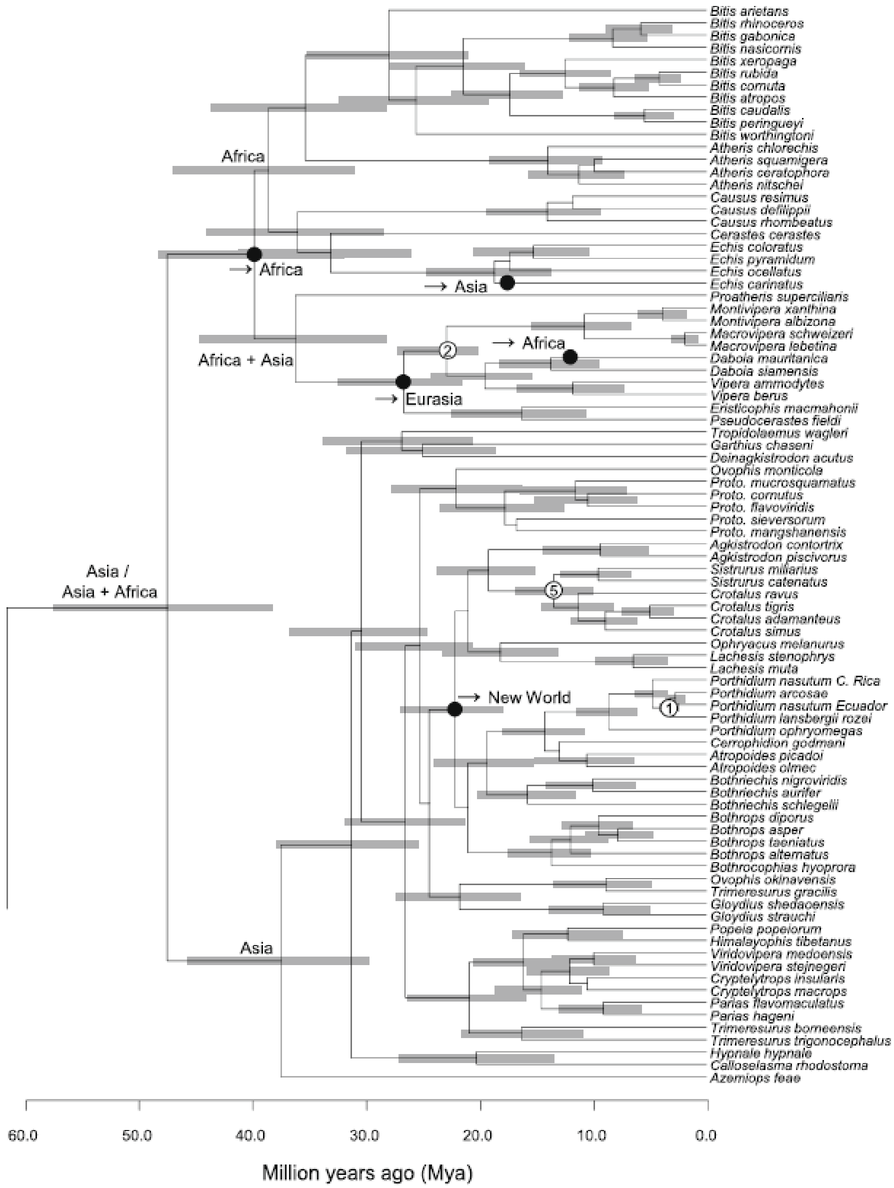

Fig. 12 – Phylogenetic time-tree of vipers with important intercontinental transitions highlighted. Taken from (Wüster et al., 2008).

4.2. Biogeography of Viperinae and Interesting Radiations within the Subfamily

The centres of the diversity of the subfamily Viperinae lie predominantly in Africa and the Western Palearctic. Some species, however, have expanded further East, with *Daboia siamensis* reaching all the way to Lesser Sunda Islands and *Vipera berus* reaching the Pacific coast of Eastern Russia (Roll et al., 2021). There are three both phylogenetically and biogeographically distinct clades, as described in the "phylogenetic part" of the thesis. The genera *Atheris*, *Bitis*, *Proatheris*, *Montatheris* and *Causus* are found almost exclusively in the Afrotropics, *Echis* and *Cerastes* occur mostly in the recently defined realm of Saharo-Arabia, while the rest of the genera (*Daboia*, *Eristicophis*, *Macrovipera*, *Montivipera*, *Pseudocerastes*, *Vipera*) is distributed in the Western Palearctic, with occasional species expanding into other zoogeographical realms (Wüster et al., 2008; Holt et al., 2013; Šmíd & Tolley, 2019; Roll et al., 2021).

The arboreal genus *Atheris* has diversified mostly along the East African Rift (EAR). This is due to the gradual aridification of East Africa since approximately 15 Ma that has fragmented the montane forests that members of this genus inhabit. Several species are also found in western Africa, in the lowland forests of the Congo Basin and the coast of the Gulf of Guinea. Some are small-area endemics, while others inhabit relatively large distribution ranges (Menegon et al., 2014; Roll et al., 2021).

The genus *Bitis* has radiated mainly in The Cape in southern Africa and in coastal Namibia, with some species being restricted to the fynbos biome, while others have become desert specialists with corresponding morphological adaptations. The morphological diversity in this genus manifests itself in the fact that both the smallest (*B. schneideri*) and the largest (*B. rhinoceros*) species of the subfamily Viperinae belong to this genus. Other species of the genus inhabit African lowland forests and montane forests along the EAR; however, open habitats are considered an ancestral habitat. *Bitis arietans* is the only species of the Subsaharan clade venturing out of Subsaharan Africa (though only marginally) with relict populations in Morocco, northern Niger and the Arabian Peninsula (Wittenberg et al., 2015; Barlow et al., 2019; Šmíd & Tolley, 2019; Ceríaco et al., 2020).

The wide distribution of the genus *Echis* makes its biogeography very interesting, especially considering the geological activity of the region where the distribution area lies. A study focused on the historical biogeography of *Echis* showed that the early diversification of the genus indeed corresponds with the major geological events in Afro-Arabia, specifically the collision of the Arabian and Anatolian tectonic plates and the formation of the Red Sea (Pook et al., 2009).

The Mediterranean and Anatolia host a radiation of the genus *Vipera* that includes over 20 species. This could be given the structured geomorphology of the area which was even more articulated in the late Miocene as substantial part of eastern Europe and western Asia were flooded by the Paratethys mega-lake. It is presumed that the Messinian Salinity Crisis (MSC) also played a role in the diversification dynamics as the divergence times of *V. latastei* and *V. monticola* correspond with the end of MSC (Šmíd & Tolley, 2019; Freitas et al., 2020; Martínez-Freiría et al., 2021; Palcu et al., 2021). In the closely related genus *Montivipera*, distributed predominantly in the high altitudes of Anatolia and the Iranian Highlands, it was shown that the diversification was driven mainly by Plio-Pleistocene climatic oscillations (Stümpel et al., 2016). I believe that it is safe to assume that these oscillations have to some degree also influenced the specific and subspecific diversity of the genus *Vipera*.

4.3. Azemiopinae, Old World Crotalinae and Their Radiations

Both Azemiopinae and the Old World Crotalinae are distributed predominantly in tropical Asia. The two species of the genus *Azemiops* inhabit forests of northern Vietnam and south-eastern China. Asian crotalines have diversified mostly in southeast and eastern Asia, a substantial diversity can, however, be found in other parts of the continent as well, ranging from the tropics to the temperate zone. Few species of the genus *Gloydius* can be found even in the Western Palearctic (Roll et al., 2021).

The most species-rich radiation, with over fifty species, is found in the genus *Trimeresurus*. While the taxonomy and systematics of the genus have been subjects of many studies, the biogeographical context of this radiation has not been thoroughly inspected yet. However, it is probable that the sea-level oscillations during the Pliocene and Pleistocene in the region, especially around the Malay Archipelago, have contributed to the diversification of this lineage, together with the orogenic events in Asia during the Tertiary (Tu et al., 2000; Wüster et al., 2008; David et al., 2011; Sumontha et al., 2021). The turbulent geological history of southern and southeast Asia during the Tertiary, caused by the collision of the Indian and Eurasian tectonic plates that resulted in the formation of the Himalayas and adjacent mountain ranges, also seems to have contributed to the diversification of other relatively species rich genera of Crotalinae in the region, *Gloydius*, *Protobothrops* and *Ovophis* (Guo et al., 2016; Shi et al., 2021).

4.4. New World Radiation

Crotalines crossed into North America through Beringia approximately 25 – 20 Ma and have subsequently radiated rapidly into more than 150 species that are extant there today. All recent molecular studies agree that the radiation is monophyletic, meaning that the family has crossed into the New World just once. This hypothesis is further supported by the fossil findings (Wüster et al., 2008; Alencar et al., 2016). However, other, “unsuccessful”, expansions, resulting in the lineage becoming extinct, cannot be completely ruled out (Alencar et al., 2018). Today, pit vipers are distributed throughout Americas from southern

Canada and reaching southern Patagonia, where *Bothrops ammodytoides* can be found. No other snake species lives further south (Roll et al., 2021).

Within the radiation, the genera *Crotalus*, *Sistrurus* and *Agkistrodon*, that are often considered to comprise one monophyletic clade, have diversified mostly in temperate and subtropical North America, with *Crotalus* originating probably in the Mexican highlands and then radiating mainly during the Miocene and Pliocene along the Rocky Mountains and Sierra Madre mountains ranges in Mexico (Wüster et al., 2008; Blair & Sánchez-Ramírez, 2016; Blair et al., 2019).

The genus *Bothriechis* is distributed mainly throughout montane cloud forests of Central America. The complicated geological history of the region with unstable tectonics and rich volcanic activity has caused the genus to undergo reticulate evolution, leading to conflicting phylogenies when using different genetic markers (Mason et al., 2019).

4.4.1. Expansion into South America

Many genera of the New World radiation have reached South America, as the Great American Biotic Interchange (GABI) played a major role in the process. *Crotalus* is represented in the continent by three closely related species, *C. durissus*, *C. unicolor* and *C. vegrandis*, which have diverged from their ancestors approximately in the time of GABI (ca 2.7 Ma ago). However, some authors consider the latter two to be subspecies of *C. durissus* (Carbajal-Márquez et al., 2020; Velasco et al., 2022). Other genera, such as *Bothriechis*, *Lachesis* and *Porthidium*, have reached South America as well, but each is represented in the continent only by one or two species (Wüster et al., 2008; Alencar et al., 2016; Roll et al., 2021).

However, one lineage, consisting of the genera *Bothrops* and *Bothrocophias*, has reached the continent well before GABI, and had started radiating approximately 20 – 15 Ma ago, despite the first known fossil being known from as late as the late Miocene (ca 9 – 7 Ma ago) (Wüster et al., 2008; Albino & Brizuela, 2014; Alencar et al., 2016). This serves as a piece of evidence for a land bridge between Central and South America emerging during early to middle Miocene (Albino & Brizuela, 2014). The monophylum has since diverged into more than fifty species with a wide diversity of niches – some species are arboreal and inhabit tropical rainforests (like *Bothrops bilineatus*), while *B. ammodytoides* can be found in temperate areas of Patagonia. It is presumed that the emergence of the dry regions of Cerrado and Caatinga that have separated the Amazon and Atlantic forests could have played a significant role in the diversification of the lineage. Interestingly enough, one species (*Bothrops asper*) has "returned" to Central America, presumably during the GABI event (Pontes-Nogueira et al., 2021).

4.5. Threats and Conservation of Vipers

The Anthropocene, defined as the period of a substantial influence of human activities on the environment (Steffen et al., 2011), has covered minimal part of the evolutionary history of the Viperidae family. However, the human impact can be a nonnegligible influence on the species diversity today. While no species of vipers have been declared extinct, some, like *Tropidolaemus huttoni* and *Cerastes boehmei*, have not been seen since their description. Several factors make viper species more susceptible to extinctions than species of most other reptile lineages would be. Indeed, while vipers comprise only 9 % of all snake species, they make up about 17 % of those considered threatened by IUCN Red List (Maritz et al., 2016; IUCN, 2022).

The solenoglyphous dentition, considered to be one of the key innovations responsible for their evolutionary success, has in the age of humans "backfired" as vipers are in huge parts of their distribution area persecuted because of the risk of envenomation they pose to local human communities. Other factors are also at play. Due to the attractiveness of some species like *Bitis nasicornis*, *B. gabonica*, *Atheris* spp. or *Lachesis* spp., collection for pet trade can have massive impact on local populations. Moreover, some species like *Gloydius himalayanus* are used in traditional medicine. However, while individual collections and killings of viperids can pose a significant danger to some populations, the larger threat is ultimately habitat fragmentation and destruction (Maritz et al., 2016).

In response to these threats, IUCN Viper Specialist Group was created to evaluate the conservation status of all viper species and bring forward an "Action Plan" to globally coordinate conservation efforts for viperid snakes (Maritz et al., 2016; viperconservation.org, 2022). Moreover, several projects focused on conservation of individual species around the world have been established. Examples of these can be the Bushmaster Conservation Project in Costa Rica, focusing on research and conservation of the genus *Lachesis*, or The Hungarian Meadow Viper Conservation Centre, established to increase the population numbers of *Vipera ursinii rakosiensis* (Péchy et al., 2015; bushmasterproject.com, 2022). Regarding the threat posed by pet trade, eight species are now listed in the CITES appendices, however the view of CITES on non-validity of some species (e.g. *Daboia siamensis*) does not correspond with the current consensus (IUCN, 2022).

5. Summary

Vipers are without a doubt one of the most fascinating snake families and thanks to a number of recent studies, we are now beginning to understand their evolutionary history and mechanisms behind it. However, there are still many questions left, and the evolutionary remarkableness and medical importance of the family warrant us answering them.

From a phylogenetic point of view, discussions can still be held about positions of the morphologically rather ancestral genera *Causus* and *Azemiops*. Phylogenetic reconstructions of the New World radiation are also far from showing clear and unified results. As all the recent molecular phylogenies of the family have been created using phylogenetic analyses of only a few genes, many of the phylogenetic mysteries could be solved by using more advanced phylogenetic methods, which would give us more accurate reconstruction of the evolutionary history. Analysis of the ultraconserved (UCE) loci could be an example of such a method, and I would like to use this approach as a basis for my Master's thesis. Precise reconstruction of the phylogeny of viperids is needed to understand the evolution of the many-times-mentioned key innovations. It would definitely be interesting to see how for example reproduction modes originate and disappear throughout the evolutionary history.

Other questions arise when comparing diversification dynamics of viperids and other snake taxa. Alencar et al. (2018) pose a question why there are not any aquatic life forms evolved within the family. In my opinion, this could be explained by the several adaptations vipers have for colder and thus higher altitude habitats, resulting in sort of an ecological preference for those. However, large areas of wetland habitat and river deltas which could present an opportunity for an evolutionary shift to an aquatic lifestyle are mostly found in lowlands. Here, vipers are, in terms of species diversity, "overrun" by other snake families, mostly Colubridae and Elapidae, where aquatic and semiaquatic lifeforms can be found. Subsequently, viper species would also be less likely to reach coastlines and thus the probability of evolving a marine life form (as we can see it in e.g. elapids) would also be reduced.

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