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Limnodynastes cameronganti from Glenaire, west of Apollo Bay, Victoria, Australia. Photo by Raymond Hoser.

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Contents

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***Crinia (Ranidella) signifera* from Johanna, Victoria, Australia.**

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Publishes original research in printed form in relation to reptiles, other fauna and related matters, including classification, ecology, public interest, legal, captivity, "academic misconduct", etc. It is a peer reviewed printed journal published in hard copy for permanent public scientific record in accordance with the *International Code of Zoological Nomenclature* (Ride *et al.* 1999 as amended online since), with sizeable print run and global audience and high impact.

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Litter, plastic sheets and rubbish. It's not necessarily an eco-disaster for all species!

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ABSTRACT

Human hard rubbish in the form of old building materials, sheets of iron and the like have long been known as habitat for reptiles in particular (Hoser 1996).

This paper details use of plastic sheets as a refuge and habitat for multiple species of frogs in Victoria, Australia, including as a potential springboard for range expansions.

INTRODUCTION

While doing field-work across Victoria in the years 2021-2022, I had cause to search for reptiles and frogs on private properties in numerous parts of the State.

In three separate situations frogs were found sheltering within piles of dumped plastic bags or sheeting.

This paper details the three relevant finds and implications of them.

MATERIALS AND METHODS

Myself and Daniel Mannix of the Victorian Dog Training Academy have been training dogs to avoid snakes (Snake Avoidance, Australian registered trademark, TM No. 1869367).

Details at http://www.dogsnakeavoidancetraining.com.au (as of 1 Dec 2022).

This is commonly done on private farming properties in rural parts of the State of Victoria, Australia.

It is routine for owners of the properties to ask me to do a sweep of the property to remove snakes near homes and buildings and/or to inspect the place to assess likelihood of snake encounters and possible steps to remove favourable habitat for snakes near dwellings.

In the process, I survey for other fauna, including small reptiles and frogs, noting that some were until recently undescribed in this State, with several new species of frog and reptile from Victoria named for the first time as recently as 2020-2022 (e.g. Hoser 2020a-c, 2022a-c), some of those species first being flagged as new to science, directly from observations made in field surveys as just outlined.

The surveying is done opportunistically by way of (usually) lifting bits of hard cover looking for hiding animals or less often by direct observation of specimens in the open.

In terms of this paper, three instances of frogs hiding amongst plastic sheeting is given.

The first case was in March 2021, and the second two in November 2022.

RESULTS

On 8 March 2021, at a farm at 1143 Kinglake-Glenburn Road, Glenburn, in the Murrundindi Shire, Victoria, I lifted a mass of black plastic garbage bags which in turn contained other materials. Within this mass were two *Geocrinia victoriana* (Boulenger, 1888), being a male and female (not together, but presumed to be a pair, as no others were found, both were adult and they were found within 30 cm of each other). On the west side of the pile of debris was an old caravan that had been there for years and the east side was bare ground and exposed to the morning to midday sun.

The thermal position of the mass meant it got the morning warmth from the sun, but was shaded in the warmest part of the day and afternoon.

Furthermore the plastic mass had bodies of water in the folds. Noting the tiny size of adult *Geocrinia victoriana* it is likely that in the absence of this water in the plastic masses that the frogs could not have survived here. They did appear to need the high humidity immediately adjacent in the same cracks or crevices.

A search of other parts of the farm property failed to yield any other frogs. There was no other plastic garbage bags or anything else that held water as such on the property. The only habitat apparently suitable for the frogs at that time and place was the man-made rubbish.

The weather that day was dry, cool, windy and partly cloudy at the relevant times.

In the mid-morning of 1 November 2022, I stopped on the side of the Great Ocean Road at Johanna, Victoria, 3238 (in the western Otway Ranges) and searched among a large amount of roadside rubbish.

Included was several masses of thick black plastic sheeting that was folded over itself. Inside these sheets were found two adult *Crinia* (*Ranidella*) *signifera* Girard, 1853. The two frogs were found separately in two sheet masses and were 1 male and 1 female. Due to the distance apart, they were not presumed to be

a pair.

No frogs were found under other cover. The sheets of plastic these frogs were found within also contained substantial amounts of standing water within the folds. The weather that day was cool, mainly cloudy and dry.

On the same date, in the early afternoon, at a property at 3430 Great Ocean Road, Glenaire, I lifted a disused blow-up plastic baby pool in a ditch. Within the folds of plastic was sheltering an adult *Limnodynastes cameronganti* Hoser, 2020. Like the two previous cases, there was standing pools of water within the folds of the plastic approximately where this frog was sheltering. The rest of the nearby parts of the property was dry. A nearby farm dam had no obvious daytime hiding spots for frogs.

No other frogs were located on that property that day.

The weather was as for the morning, although later that day (at the time we left the property at about 4.30 PM) torrential rain hit the area.

DISCUSSION

In all three preceding cases, frogs were found hiding in plastic sheeting of some form that held standing water and gave frogs a safe and hydrated hiding place. In the wild state such places are uncommon except near water bodies like dams and the like. However farm dams and the like often lack stones, logs or other cover that are part submerged in water and allow frogs to hide in moist places by day.

For larger frogs, it may be possible to survive extended periods in dry places. However this luxury is not available to tiny species such those within the genera *Geocrinia* Blake, 1973 or *Crinia* Tschudi, 1838.

In these cases the disused plastic bags that were dumped as rubbish or the disused plastic sheets were probably the only potentially available habitat for these species in the relevant places and times.

Geocrinia sensu lato (as defined by Hoser 2020c) is a genus comprising species with constrained distributions and appear constrained by regions of dryness or aridity.

Use of man-made rubbish in the form of plastic bags, sheets and the like that hold rainwater in folds may well allow these species to survive and expand in areas they previously would not have survived in.

As a result, man-made rubbish in the form of plastic garbage bags, plastic sheeting and the like could be a boon for tiny frog species within the genera *Geocrinia*, *Crinia* and other morphologically similar tiny frogs.

The moan of environmentalists that plastics take many years to break up and decompose may in fact be an aid to the short to medium term survival of some populations of frogs within these genera.

Besides enabling frogs the ability to physically invade places they would otherwise not be able to survive in, transportation by people of plastic sheeting with frogs contained within the sheets may be a means by which frogs can be translocated hundreds of kilometres to places they would otherwise never get to.

This could mean in the future species from one part of Australia could become feral and invasive in another.

In the short to medium term, government wildlife departments should be spending some of their money issuing adverts and regular warnings of the potential perils of inadvertently translocating frogs, including within plastic sheeting.

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Hoser, R. T. 2020b. For the first time ever! An overdue review and reclassification of the Australasian Tree Frogs (Amphibia: Anura: Pelodryadidae), including formal descriptions of 12 tribes, 11 subtribes, 34 genera, 26 subgenera, 62 species and 12 subspecies new to science. *Australasian Journal of Herpetology* 44-46:1-192.

Hoser, R. T. 2020c. 3 new tribes, 3 new subtribes, 5 new genera, 3 new subgenera, 39 new species and 11 new subspecies of mainly small ground-dwelling frogs from Australia. *Australasian Journal of Herpetology* 50-51:1-128.

Hoser, R. T. 2022a. Hiding in plain sight. A previously unrecognized biogeographical barrier in Australia formed by an event of biblical proportions. Five new species of skink lizard from south-west Victoria, three more closely related species from New South Wales and another from South Australia. *Australasian Journal of Herpetology* 56:3-21.

Hoser, R. T. 2022b. The inevitable split up of the common Australian skink lizard *Allengreerus delicata* AKA *Lampropholis delicata* into resurrected and new species (Reptilia: Squamata: Scincidae). *Australasian Journal of Herpetology* 57: 28-52.

Hoser, R. T. 2022c. Greater diversity of skink species in south-east Australia than previously realized: *Carinascincus* Wells and Wellington, 1985 sensu lato is further divided. *Australasian Journal of Herpetology* 59:48-64.

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CONFLICT OF INTEREST

None.

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A new Viper species from Croatia (Reptilia: Squamata: Serpentes: Viperidae: *Pelias*).

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ABSTRACT

This paper formally names a new species of viper from Croatia, Europe as *Pelias cathrynmatteoae sp. nov*..

This range-restricted taxon has been known as distinct for some years. It is most closely related to *Pelias ursinii* Bonaparte, 1835, a species placed by most publishing authors in the genus *Vipera*

Laurenti, 1769, or alternatively the nominate taxon best known as *Vipera ursinii rakosiensis* Mehely, 1893, herein treated as a full species, that being the next most closely related species.

The putative taxa *Vipera ursinii macrops* Mehely, 1911 and *Vipera ursinii moldavica* Nilson, Andren and Joger, 1993 are treated herein as subspecies of *Vipera rakosiensis* based on their limited divergence from that taxon, but all are also included herein in the genus *Pelias* Merrem 1820.

P. cathrynmatteoae sp. nov. as formally named herein has also at times been confused with putative *P. ursinii macrops* Mehely, 1911.

P. cathrynmatteoae sp. nov. (type locality Velebit, Croatia) is split into two subspecies with *P. cathrynmatteoae kapelaensis subsp. nov*. occurring in the Kapela Range (part of the northern Dinaric Alps).

A subspecies of *P. ursinii* from far south-eastern France, east of the Durance River is also formally named for the first time as *P. ursinii alpesdehautensis subsp. nov.*. It is a distinctly different subspecies to the previously named *P. ursinii wettsteini* Knoepffler and Sochurek, 1955, with a type locality of den Montagne de Lure, Bases Alpes, south-east France and occurring west of the Durance River.

The southern population of *P. graeca* (Nilson and Andren, 1988) is formally named as the subspecies *P. graeca vardousiaensis subsp. nov*..

With limited distributions, combined with a strong interest in vipers among herpetologists, it would make sense for viable captive populations of the relevant taxa to be established to protect against unforseen calamity or event that may exterminate those in the wild.

Keywords: Snake; viper, taxonomy; nomenclature; new species; vipers; Croatia; Europe; *Pelias*; *Vipera*; *Acridophaga*; *ursinii*; *wettsteini*; *rakosiensis*; *macrops*; *moldavica*; *graeca*; new species; *cathrynmatteoae*; new subspecies; *kapelaensis*; *alpesdehautensis*; *vardusiaensis.*

INTRODUCTION

In spite of centuries of scrutiny by herpetologists, there remain numerous undescribed species of vipers.

In the past 2 decades (post year 2000), dozens of species and subspecies of viper and pitviper species have been formally named from most parts of their known distribution, including Spain, Greece, Turkey, many parts of Africa, South-east Asia, the USA, Mexico and central America.

New genera have also been named in both old and new world and for both vipers and pitvipers.
Species and/or subspecies of viper formally described in the preceding 10 years (2012-2022) include the following:

Adelynhoserserpenae borealis (Tepos-Ramirez, Flores-Villela, Velasco, Lara, Garcia-Rubio and Jadin, 2021)
Adelynhoserserpenae wellsi Hoser, 2013
Atheris hetfieldi Ceraico, Marques and Bauer, 2020
Atheris mongoensis Collet and Trape, 2020
Azemiops kharini Orlov, Ryabov and Nguyen, 2013
Bitis harenna Gower, Wade, Spawls, Böhme, Buechley, Sykes and Colston, 2016
Bitis (Klosevipera) kajerikbulliardi Hoser, 2013
Bitis (Klosevipera) swilae Hoser, 2013
Bitis benjaminswilei Hoser, 2022
Bitis brianwallacei Hoser, 2013

Bitis lourenceklosei Hoser, 2013
Bitis matteoae Hoser, 2013
Bitis oflahertyae Hoser, 2013
Bitis pintaudii Hoser, 2013
Bitis tomcottoni Hoser, 2013
Bothriechis guifarroi Townsend, Medina-Flores, Wilson, Jadin and Austin, 2013
Bothriechis nubestris Doan, Mason, Castoe, Sasa and Parkinson, 2016
Bothrops germanoi Barbo, Brooker, Duarte, Chaluppe, Portes-Junior, Franco and Grazziotin, 2022
Bothrops jabrensis Barbo, Grazziotin, Pereira-Filho, Freitas, Abrantes and Kokubum, 2022
Bothrops lenhoseri Hoser, 2013
Bothrops maccartneyi Hoser, 2013
Bothrops mexicoiensis Hoser, 2013
Bothrops monsignifer Timms, Chaparro, Venegas, Salazar-Valenzuela, Scrocchi, Cuevas, Leynaud and Carrasco, 2019
Bothrops oligobalius Dal Vechio, Prates, Grazziotin, Graboski and Rodrigues, 2021
Bothrops otavioi Barbo, Grazziotin, Sazima, Martins and Sawaya, 2012
Bothrops sazimai Barbo, Gasparini, Almedia, Zaher, Grazziotin, Gusamo, Ferrarini and Sawaya, 2016
Bothrops sonene Carrasco, Grazziotin, Cruz-Farfan, Koch, Ochoa, Scrocchi, Leynaud and Chaparro, 2019
Caudisona ehecatl (Carbajal-Marquez, Cedeno-Vazquez, Martinez-Arce, Neri-Castro and Machkour-M'Rabet, 2020)
Caudisona mictlantecuhtli (Carbajal-Marquez, Cedeno-Vazquez, Martinez-Arce, Neri-Castro and Machkour-M'Rabet, 2020)
Caudisona evatti Hoser, 2020
Causus perkinsi Hoser, 2013
Causus rasmusseni Broadley, 2014
Cerrophidion sasai Jadin, Townsend, Castoe and Campbell, 2012
Cerrophidion wilsoni Jadin, Townsend, Castoe and Campbell, 2012
Cottonus tomcottoni Hoser, 2020
Craspedocephalus peltopelor Mallik, Srikanthan, Ganesh, Vijayakumar, Campbell, Malhotra and Shanker, 2021
Craspedocephalus travancoricus Mallik, Srikanthan, Ganesh, Vijayakumar, Campbell, Malhotra and Shanker, 2021
Daboia (Oxyadaboia) oxyi Hoser, 2022
Daboia (Oxyadaboia) sloppi Hoser, 2022
Daboia crottyi Hoser, 2022
Gloydius angusticeps Shi, Yang, Huang, Orlov and Li, 2018
Gloydius huangi Wang, Ren, Dong, Jiang, Shi, Siler and Che, 2019
Gloydius lipipengi Shi, Liu, Giri, Owens, Santra, Kuttalam, Melvan, Guo and Malhotra, 2021
Gloydius rickmersi Wagner, Tuitenko, Borkin and Simonov, 2015
Gloydius rubromaculatus Shi, Li and Liu, 2017
Gloydius swild Shi, Liu, Giri, Owens, Santra, Kuttalam, Melvan, Guo and Malhotra, 2021
Macrocerastes funki Hoser, 2013
Macrocerastes hoserae Hoser, 2013
Macrocerastes wellingtoni Hoser, 2013
Macrovipera razii Oraie, Rastegar-Pouyani, Khosravani, Moradi, Akbari, Sehhatisabet, Shafiei, Stumpel and Joger, 2018
Matteoea dorosioi Hoser, 2020
Matteoea matteoae Hoser, 2020
Matteoea sommerichi Hoser, 2020
Matteoea polisi (Meik, Schaack, Flores-Villela and Streicher, 2018)
Matteoea thalassoporus (Meik, Schaack, Flores-Villela and Streicher, 2018)
Montivipera europa Hoser, 2016
Montivipera snakebustersorum Hoser, 2016
Montivipera yeomansi Hoser, 2016
Ophryacus smaragdinus Grunwald, Jones, Franz-Chavez and Ahumada-Carillo, 2015
Pelias sakoi Tuniyev, Avci, Tuniyev, Ilgaz, Olgun, Petrova, Bodrov, Geniez and Teynie, 2018
Pelias walser (Ghielmi, Menegon, Marsden, Laddaga and Ursenbacher, 2016)
Piersonus bartletti Hoser, 2020
Protobothrops dabieshanensis Huang, Pan, Han, Zhang, Hou, Yu, Zheng and Zhang, 2012
Protobothrops himalayanus Pan, Chettri, Yang, Jiang, Wang, Zhang and Vogel, 2013
Protobothrops kelomohy Sumontha, Vasaruchapong, Chomngam, Suntrarachun, Pawangkhanant, Sompan, Smits, and Kunya Chanhome, 2020
Sayersus wellingtoni Hoser, 2020
Sayersus wellsi Hoser, 2020
Smythus smythi Hoser, 2020
Smythus teesi Hoser, 2020
Trimeresurus ashokcaptaini Hoser, 2022
Trimeresurus arunachalensis Captain, Deepak, Pandit, Bhatt and Athreya, 2019
Trimeresurus caudornatus Chen, Ding, Vogel and Shi, 2020
Trimeresurus davidi Chandramouli, Campbell and Vogel, 2020
Trimeresurus gunaleni Vogel, David and Sidik, 2014
Trimeresurus guoi Chen, Shi, Vogel and Ding, 2021
Trimeresurus kuiburi Sumontha, Suntrarachun, Pauwels, Pawa-Ngkhanant, Chomngam, Iamwiriyakul and Chanhome, 2021
Trimeresurus mayaae Rathee, Purkayastha, Lalremsanga, Dalal, Biakzuala, Muansanga and Mirza, 2022
Trimeresurus paracaeruleus Hoser, 2022
Trimeresurus salazar MIRZA, BHOSALE, PHANSALKAR, SAWANT, GOWANDE & PATEL, 2020
Trimeresurus yingjiangensis CHEN, ZHANG, SHI, TANG, GUO, SONG & DING, 2019
Uropsophus campbelli (Bryson Jnr, Linkem, Dorcas, Lathrop, Jones, Alvarado-Diaz, Grunwald and Murphy, 2014)
Uropsophus elfakhariorum Hoser, 2020
Uropsophus euanedwardsi Hoser, 2020
Uropsophus hammondi Hoser, 2020
Uropsophus oxyi Hoser, 2020
Uropsophus strimplei Hoser, 2020
Uropsophus swileorum Hoser, 2020
Uropsophus tlaloci (Bryson Jnr, Linkem, Dorcas, Lathrop, Jones, Alvarado-Diaz, Grunwald and Murphy, 2014)
Uropsophus valentici Hoser, 2020
Vipera britoi Hoser, 2015
Vipera hoserae Hoser, 2015
Vipera veloantoni Hoser, 2015
Vipera wellingtoni Hoser, 2015
Vipera wellsi Hoser, 2015

(The species in the above list and relevant publications they were first published in can be found at http://www.zoobank.org, with most relevant full papers available for download as pdfs at http://www.herp.net).

Members of the Wolfgang Wüster gang of thieves as detailed in Hoser (2015a-f) have coined non-ICZN names for some of the preceding viper taxa and these illegal names are not listed here. They are listed in various synonyms lists.

The International Commission on Zoological Nomenclature (ICZN) has published scathing rulings against the Wüster gang of thieves several times (ICZN 1991, 2001, 2021).

For many years it has been known that the so-called Meadow Viper, generally known in herpetology as *Vipera ursinii* (Bonaparte, 1835), but herein placed in *Pelias* Merrem, 1820 (along with all closely related viper species subject of this paper), mainly from southern Europe, consists of several morphologically distinct forms.

Numerous names have been coined, for the various localized forms as listed by McDiarmid *et al*. (1999), with some of these being generally recognized as subspecies.

Others have been synonymised.

While the consensus among herpetologists has been that the viperidae, including *P. ursinii* has been over-split by herpetologists *sensu* Freitas *et al*. (2020) the results of the phylogeny they produced revealed that while over-splitting had certainly occurred, there remained a number of potentially unnamed species and/or subspecies.

Included among these were a population of putative *P. ursinii* (type locality Abruzzi, Ascole Province, Italy), from Croatia, for which there was no available name, as well as populations of putative "*Vipera ammodytes* (Linnaeus, 1758)" (type locality Zadar, Croatia) from other parts of eastern Europe, in particular southern Greece.

This paper deals primarily with the taxon from Croatia, most similar to *P. ursinii.*

Five unnamed species and 8 previously unnamed subspecies in the "*Vipera ammodytes* (Linnaeus, 1758)" complex are formally named in a separate paper published at the same time as this one.

As of 2022, most publishing authors agree with Freitas *et al*. (2020) in recognizing nominate *P. ursinii* as a full species as well as each of *Vipera ursinii rakosiensis* Mehely, 1893 (type locality near Budapest, Hungary), *Vipera ursinii macrops* Mehely, 1911 (type locality Korita, Herzegovina) and *Vipera ursinii moldavica* Nilson, Andren and Joger, 1993 (type locality Valeui de David, Jasi, Romania) as subspecies, but there being no other valid subspecies.

The divergent "*Vipera ursinii graeca* Nilson and Andren, 1988" has most recently been treated by most herpetologists as a separate species and is also herein treated as in the genus *Pelias*.
(*Pelias* Merrem, 1820 has the type species of *Coluber berus* Linnaeus, 1758)

Other subspecies have been proposed by various authors, (as listed by McDiarmid *et al*. 1999), but not generally accepted or used in herpetology.

The phylogenies of Gvozdík *et al*. (2011), Ferchaud *et al.* (2011, 2012) and Freitas *et al*. (2020), assumed here to be accurate, showed three divergent species-level lineages in the complex, these being lineages with a divergence of 2 MYA or more. These were *P. ursinii*, another listed as *Vipera ursinii ssp.* (being a population until now usually treated as putative "*Vipera ursinii macrops* Mehely, 1911", to which it is geographically proximal to and morphologically similar to), and a group of three closely related putative taxa being, "*Vipera ursinii rakosiensis* Mehely, 1893" (type locality near Budapest, Hungary), "*Vipera ursinii macrops* Mehely, 1911" (type locality Korita, Herzegovina) and "*Vipera ursinii moldavica* Nilson, Andren and Joger, 1993" (type locality Valeui de David, Jasi, Romania) all having diverged from one another less than 1 MYA, meaning that all these should best be treated as a single species.

Gvozdík *et al*. (2011) got similar results, although their putative "*Vipera ursinii macrops*" was in fact the unnamed taxon from the Velebit Mountains, Croatia as opposed to type form of "*V. ursinii macrops*" from further south in Herzegovina.

With the Croatian form of putative *Pelias ursinii* twice flagged as being divergent at the species-level a decade apart and with no one indicating an intention to formally name this taxon, the primary purpose of this paper is to formally name it so that:

1/ Science can progress, and,
2/ Wildlife conservation agencies and NGO's can manage and conserve this species.

At the same time divergent populations of French *V. ursinii* were inspected to see if more than one subspecies occurred there as inferred by morphologically divergent populations on either side of the Durance River in south-eastern France and recently published studies of Ferchaud *et al.* (2011, 2012).

Furthermore, *V. graeca* were also inspected across their relatively small range to see if any subpopulations warranted taxonomic recognition.

MATERIALS AND METHODS

All relevant literature was reviewed to confirm that the putative taxon from Croatia was in fact an unnamed species, via checks of potentially available synonyms and to confirm the taxonomy shown by Freitas *et al*. (2020) and Gvozdík *et al*. (2011) via their phylogenies. Specimens were inspected to confirm morphological divergence, including via comparison with other putative *P. ursinii* and other putative subspecies of *P. ursinii.* That is including specimens from across the known range of the species complex.

Specimens of closely related species such as *Pelias renardi* Christoph, 1861, including putative subspecies and *P. graeca* (Nilson and Andren, 1988) were also inspected and compared with the Croatian form.

Literature relevant to the taxonomy, nomenclature and conclusions within this paper included

Balija *et al.* (2020), Baron *et al.* (1993), Benyr (2016), Beshkov and Nanev (2006), Billing (1985), Billing *et al*. (1990), Bodon (2009), Böhme and Joger (1984), Bonaparte (1835), Boulenger (1893, 1896, 1913), Cabela and Tiedemann (1985), Christoph (1861), Cogălniceanu *et al.* (2013), Console *et al.* (2020), Crnobrnja-Isailovic (2001), Dely and Stohl (1989a, 1989b), Di Nicola (2019), Eiselt and Baran (1970), Ferchaud *et al.* (2011, 2012), Freitas *et al.* (2020), Garanin *et al.* (2004), Garrigues *et al.* (2005), Gebhart (2020), Gemel *et al.* (2019), Ghira (2007), Golay *et al.* (1993), Grillitsch (2010), Gruber (2009), Gvoždík (2011), Hallmen (2015), Halpern and Péchy (2010), Ride *et al*. (1999), Jelić *et al.* (2013), Joger *et al.* (1992, 2007), Kabisch (1966), Kabisch and Belter (1968), Kammel (1992a, 1992b), Knoepffler and Sochurek (1955), Korsós *et al.* (2008), Kramer (1961), Krecsak (2007), Krecsák and Tóth (2009), Krecsák and Zamfirescu (2001), Kucharzewski (2011), Kukuskin (2009), Kunz (2015), Kwet (2010), Kwet and Trapp (2014a, 2014b), Lambert (2002), Lantermann and Lantermann (2010), Linnaeus (1758), Luef (2014), Mallow *et al.* (2013), Martínez-Freiría *et al.* (2020), McDiarmid *et al.* (1999), Méhely (1893, 1894, 1911), Merrem (1820), Mizsei *et al.* (2016, 2017), Naulleau (1987), Nilson and Andrén (1988, 2001), Nilson *et al.* (1988, 1993, 1995), Phelps (2010), Reading *et al*. (2010), Reuss (1924, 1927a, 1927, 1929, 1933), Ride *et al*. (1999), Schlüter (2009), Schwederski and Trutnau (2017), Schweiger (2009, 2012), Shine and Madsen (1994), Sigg (1987, 1990), Sindaco *et al.* (2000, 2013), Sos (2008), Sterijovski (2006), Strugariu (2008), Tabachishina *et al.* (2002), Tiedemann and Grillitsch (1999), Tomović *et al*. (2004, 2008), Török (2007), Tóth *et al.* (2005), Trapp (2006, 2007, 2011, 2014), Trutnau (1975), Tuniyev *et al.* (2010), Újvári *et al.* (2000, 2005), Üveges *et al.* (2012), Vancea *et al*. (1985), Vedmederja *et al.* (1986), Veith (1991), Venchi and Sindaco (2006), Wagner *et al*. (2015), Wallach *et al*. (2014), Werner (1894), Woerkom (1987), Zinenko *et al*. (2015) and sources cited therein.

RESULTS

The relevant species in the *P. ursinii* complex are all retained in the genus *Pelias* Merrem, 1820 (type species *Coluber beras* Linneaus, 1758) based on a divergence from *Vipera* Laurenti, 1768 (type species *Vipera francisci redi* Laurenti, 1768 = *Vipera aspis* (Linnaeus, 1758)) of about 15 MYA based on the phylogeny published by Frietas *et al*. (2020).

The Croatian population of putative *P. ursinii* is not just genetically divergent from all other named forms, but also morphologically divergent and separable from the others.

With a divergence of about 2 MYA from the nearest relative, being the type form of *P. ursinii* from Italy, I have had no hesitation in formally naming the Croatian population as a new species, being *P. cathrynmatteoae sp. nov*..

That new species is formally described below in this paper.

As mentioned in the introduction, I agree with the concept put that within the immediate *P. ursinii* complex, there are just three species, being *P. ursinii*, *P. cathrynmatteoae sp. nov*. and as the third species, the cluster of putative *P. ursinii rakosiensis*, *P. ursinii macrops* and *P. ursinii moldavica.*

As *P. ursinii rakosiensis* is the oldest of the three relevant and available names, it is the name that carries the species.

The latter two names are applied to their respective populations as subspecies of *P*. *rakosiensis* as a species distinct, separate and divergent from *P. ursinii.*
This means *P. ursinii* is now confined to Italy and nearby south east France.

Pelias renardi Christoph, 1861 with a type locality of Sarepta, Russia is recognized as a single species, with the subspecies *P. renardi eriwanensis* (Reuss, 1933), *P. renardi lotievi* (Nilson, Tuniyev, Orlov, Hoggren and Andren, 1995), *P. renardi tienshanica* (Nilson and Andren, 2001), *P. renardi puzanovi* (Kukuskin, 2009) and *P. renardi bashkirovi* Garanin, Pavlov and Bakiev, 2004 also recognized as valid, based on estimated divergences of 1 MYA or less based on the published phylogenies of Gvozdík *et al*. (2011) and Freitas *et al*. (2020).

P. eriwanensis (Reuss, 1933) with a type locality in Armenia and *P. graeca* (Nilson and Andren, 1988) with a type locality of Lakmos Mountains in the southern Pindos Mountain Range in Greece are both regarded as a full species based on significant divergence from all others.

The species *P. ebneri* (Knoepffler and Sochurek, 1955) (type locality Elbrus Mountains, between Rhema and Demawend in the Elbrus Mountains, Iran) is believed to have diverged from *P. eriwanensis* about 1.4 MYA and so is also regarded as a full species.

Pelias cathrynmatteoae sp. nov. is split into two subspecies, the nominate form being from the Velebit range and the other *P. cathrynmatteoae kapelaensis subsp. nov*. from the Kapela Range (part of the northern Dinaric Alps), the two populations believed to have diverged about 500K years prior based on the phylogeny published by Ferchaud *et al.* (2012).

Not recognized at either species or subspecies level are, *P. ursinii rudolphi* (Reuss, 1924), herein treated as a synonym of *P. rakosiensis macrops* or *P. uralensis* Reuss, (1929), herein treated as a synonym of *P. renardi*,

P. ursinii wettsteini Knoepffler and Sochurek, 1955, with a type locality of den Montagne de Lure, Bases Alpes, south-east France with a divergence estimated by Ferchaud *et al.* (2012) of 0.6 MYA from the Italian population is regarded as a valid subspecies, being from the French Alps and near Alps, near the Italian border, with a type locality west of the Durance River, France.

Specimens from east of the Durance River, within France and with a similar divergence from both Italian and the other French specimens from further west (about 500K prior) are herein formally named as a morphologically diagnosable new subspecies *P. ursinii alpesdehautensis subsp. nov*..

In terms of *P. graeca* Nilson and Andren, 1988, the southern population from around Vandusia, Greece is sufficiently divergent from those in northern Greece and south Albania to warrant being recognized as a new subspecies, *P. graeca vardusiaensis subsp. nov.*.

P. anatolica Eiselt and Baran, 1970 with a type locality of Antalya, South-west Turkey is also regarded as a valid species.

The name *Acridophaga* Reuss, 1927 is available for the group at the genus level, either as a genus or subgenus, but based on divergences between other vipers and these estimated at less than 10 MYA, the name *Pelias* Merrem, 1820 (type species: *Coluber berus* Linnaeus, 1758), also available is used for the relevant species at the genus level for the purposes of this paper.

NOTES ON THE FORMAL DESCRIPTIONS THAT FOLLOW

In terms of the descriptions that follow, the following should be noted:

There is no conflict of interest in terms of this paper or the conclusions arrived at herein.

Several people including anonymous peer reviewers who revised the manuscript prior to publication are also thanked as are relevant staff at museums who made specimens and records available in line with international obligations.

In terms of the following formal descriptions, spellings should not be altered in any way for any purpose unless expressly and exclusively called for by the rules governing Zoological Nomenclature as administered by the International Commission on Zoological Nomenclature (ICZN) as published in the *International Code of Zoological Nomenclature* (Ride *et al*. 1999) ("The Code") as amended online since (ICZN 2012).

This includes if gender assignment of suffixes seems incorrect, Latinisation is wrong, apparent spelling mistakes and so on (see Article 32.5.1 of the Code).

In the unlikely event two or more newly named taxa are deemed to be the same by a first reviser, then the name to be used and retained is that which first appears in this paper by way of page priority and as listed in the abstract keywords.

Some material in descriptions for taxa may be repeated for other taxa in this paper and this is necessary to ensure each fully complies with the provisions of the *International Code of Zoological Nomenclature* (fourth edition) (Ride *et al.* 1999) as amended online since (ICZN 2012).

Material downloaded from the internet and cited anywhere in this paper was downloaded and checked most recently as of 10 August 2022 (including if also viewed prior), unless otherwise stated and was accurate in terms of the content cited herein as of that date.

Any online citations within this paper, including copied emails and the like, are not necessarily cited in the references part of this paper and have the same most recent viewing date as just given.

Unless otherwise stated explicitly, colour and other descriptions apply to living and **fully mature adult male specimens** of generally good health, as seen by day, and not under any form of stress by means such as excessive cool, heat, dehydration, excessive ageing, abnormal skin or reaction to chemical or other input.

SVL or SV means snout-vent length, TL means tail length.

While numerous texts and references were consulted prior to publication of this paper, the criteria used to separate the relevant genera, subgenera, species or subspecies has already been spelt out and/or is done so within each formal description and does not rely on material within publications not explicitly cited herein.

PELIAS CATHRYNMATTEOAE SP. NOV.

LSIDurn:lsid:zoobank.org:act:B49BED6A-8649-4D41-8DD0-BE037CA442BB

Holotype: A live specimen depicted in Figure 1 of Balija *et al.* (2020) on page 2 of 16, from southern Velebit, Croatia.

(Balija, M. L., Leonardi, A., Brgles, M., Sviben, D., Kurtowic, T., Halassy, B. and Krizaj, I. 2020. Biological Activities and Proteomic Profile of the Venom of *Vipera ursinii ssp*., a very Rare Karst Viper from Croatia. *Toxins* 2020(12)187:16 pp.)

Diagnosis: *Pelias cathrynmatteoae sp. nov.* from the Velebit Range, near the west coast of Croatia has until now been treated as a population of putative *P. ursinii* (Bonaparte, 1835), or alternatively the putative taxon *Pelias ursinii macrops* Mehely, 1911 herein treated as a subspecies of *Pelias rakosiensis* (Mehely, 1893), both of which it is proximally distributed with and morphologically similar to.

P. ursinii is herein restricted to central Italy and nearby parts of south-east France, while *P. rakosiensis* (as defined herein) is found in disjunct populations in Bosnia and Herzegovina, Montenegro, Albania, Macedonia, Hungary, Bulgaria, Moldavia and Romania.

The subspecies *Pelias rakosiensis macrops* (Mehely, 1911) is found in most parts of the Dinaric Alps within Bosnia and Herzegovina, as well as Montenegro and south to Albania.

In the Kapela Range (part of the northern Dinaric Alps), the subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* occurs, while nominate *P. cathrynmatteoae sp. nov.* is confined to the Velebit Range.

The following diagnostic information applies to adult male specimens unless otherwise stated.

Pelias cathrynmatteoae sp. nov. of both subspecies are readily separated from morphologically similar *P. ursinii* (all subspecies) and *P. rakosiensis* by the following unique combination of characters:

Tiny black barring on the posterior of the two upper labials below and behind the eye is thin and not always extending the length of the scale (upwards). Prominent blotches on either side of the flank of the body. Beige dorsum with dark brown to blackish-grey blotches, joined anteriorly and running down the midline, becoming broken posteriorly, this often forming the typical viper zig-zag configuration. On the midbody these blotches are large and circular, either merging or just broken, these becoming thinner posteriorly and elongate, becoming a zig-zag or broken zig zag.

Iris light orange.

The subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* is separated from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* by having prominent thin dark etching on the lower labials, versus not so in the nominate subspecies. The iris is also dull orange, versus bright orange. The supralabials below the eye are expanded to make the two suboculars flattened and reduced in overall size (as compared to the nominate subspecies).

In the nominate subspecies, the side blotches are usually mainly one colour only, versus obviously two colour in *P. cathrynmatteoae kapelaensis subsp. nov.*.

The nominate subspecies of *P. cathrynmatteoae sp. nov.* is depicted in life online at:

https://www.agefotostock.com/age/en/details-photo/meadow-viper-orsini-s-viper-Pelias-ursinii-lying-on-a-rock-croatia-velebit/BWI-BS265733

and

https://www.alamy.com/stock-photo-meadow-viper-orsinis-viper-Pelias-ursinii-on-the-feed-croatia-velebit-47915807.html

P. cathrynmatteoae kapelaensis subsp. nov. is depicted in life online at:

https://www.inaturalist.org/observations/126674083

The morphologically similar *P. ursinii* (Bonaparte, 1835) of the nominate subspecies from central Italy is separated from the preceding species by having heavy brown pigmentation in the iris, a beige to grey dorsal colouration (background colour) with some dark peppering. This being overlain with the dark viperine markings along the mid-dorsal line; thick dark bars or triangles at the posterior edge of the two upper labials below and behind the eye, these extending up to the top of the scale; these bars join below with equally thick dark bars on the lower labials and two over-sized suboculars. The side blotches are also prominent.

The two French subspecies of *P. ursinii* are readily separated from the nominate Italian form by having an obvious whitish-grey background colour. The side blotches are also fragmented in nature as opposed to being more-or-less squarish in the nominate subspecies.

The newly named subspecies *P. ursinii alpesdehautensis subsp. nov.* found east of the Durance River, France is separated from *P. ursinii wettsteini* Knoepffler and Sochurek, 1955 from west of the Durance River, France by having reduced blotching along the midline and narrow mid-dorsal blotches, meaning that on the mid-body these are broken up, whereas in *P. ursinii wettsteini* the same blotches are mostly broad and thick and mainly, but not always, joined to form a continuum.

Adult *P. ursinii alpesdehautensis subsp. nov.* also usually have yellowish flaring around the dark dorsal blotches, that runs into the grey background colouration, versus not so in adult *P. ursinii wettsteini.*
There is sometimes brown flaring of the blotches in adult *P. ursinii wettsteini.*
P. ursinii alpesdehautensis subsp. nov. is depicted in life online at:
https://www.inaturalist.org/observations/109925430

and

https://www.inaturalist.org/observations/57009602

P. ursinii wettsteini is depicted in life online at:

https://www.inaturalist.org/observations/29586

and
https://www.inaturalist.org/observations/38419741
and

https://www.inaturalist.org/observations/122462979

Pelias rakosiensis (Mehely, 1893) of all subspecies are separated from the two preceding species by having side blotches that are either indistinct or absent, or otherwise faded, and no prominent etching on the two upper labials below and behind the eye. Dorsum is usually beige or with a light brownish rinse through it, rather than grey and the mid-dorsal blotches are brown to dark brown, rather than black. Blotches on the mid-line of the upper and mid body are more triangular than circular as seen in both *P. cathrynmatteoae sp. nov.* and *P. ursinii.*

P. rakosiensis macrops is depicted in life online at:

https://www.inaturalist.org/observations/110557742

and

https://www.inaturalist.org/observations/24983835

P. rakosiensis rakosiensis Mehely, 1893 of the nominate subspecies from Hungary are characterised by relatively small and narrow blotches running down the midline of the dorsum, dark brown in the centres, blackish on the outer edged and with yellow flaring on the otherwise beige background. Side blotches appear as dark smudges.

The dark coloured underlying skin is particularly pronounced in this subspecies and more so than compared to all other subspecies as well as all forms of *P. ursinii.*

P. rakosiensis rakosiensis is depicted in life online at:

https://www.inaturalist.org/observations/42404735

P. rakosiensis moldavica (Nilson, Andren and Joger, 1993) is similar to *P. rakosiensis rakosiensis* as just described but has a dorsum with a whitish-grey background colour as opposed to beige.

P. rakosiensis moldavica is depicted in life online at:

https://www.inaturalist.org/observations/118043961

and

https://www.inaturalist.org/observations/96766514

The morphologically similar species, *P. graeca* Nilson and

Andren, 1988 is separated from all the preceding species by having a purplish-brown iris and by subcaudal counts. In males it is 20-27 and females is 18-21. This contrasts with 27-41 in males and 20-32 in the other preceding species.

It is further separated by having a white or pale brown venter, parietals frequently fragmented, generally fewer than 17 scale rows on posterior part of the body, 7 or 6 supralabials on each side, with the third always under the eye, posterior supralabials are noticeably smaller than the anterior ones, nasal plate often partly divided.

The two subspecies are separated as follows: There is no dark upper labial etching in the northern form being nominate *P. graeca graeca.* Southern specimens of the newly named subspecies *P. graeca vardusiaensis subsp. nov.* are separated from the nominate form by having obvious brown triangles rising from the lip in the 2 labials below and behind the eye. In the subspecies *P. graeca vardusiaensis subsp. nov.* the rear upper labials are only slightly smaller than the anterior and mid ones, versus significantly smaller in *P. graeca graeca.*

P. graeca of the nominate subspecies is depicted in life online at:

https://www.inaturalist.org/observations/20192192

and

https://www.inaturalist.org/observations/26665951

and in Nilson and Andren (1988) on pages 312 and 313.

P. graeca vardusiaensis subsp. nov. is depicted in life online at: https://www.inaturalist.org/observations/26109978

All the preceding species and subspecies are separated from all other Vipers from Europe or elsewhere, by the following unique suite of characters: Scales on crown and snout are smooth or faintly keeled; nostril in a single or irregularly divided nasal, which is separated from the rostral by a naso-rostral; rostral usually in contact with a single apical scale; supraocular large and usually extending posteriorly beyond the vertical of the posterior border of the eye; frontal and parietal shields usually well developed; a single series of scales between the eye and the labials. Snout obtusely pointed, flat above, or with the canthus slightly raised but not obviously turned up or with any kind of appendage at the end; 6 to 9 upper labials, usually 7 or 8; 19 midbody scale rows, 120-142 ventrals; 18-41 subcaudals.

The molecular phylogeny of Ferchaud *et al.* (2012) found that *P. cathrynmatteoae sp. nov.* diverged from its nearest living relative, type *P. ursinii* just under 2 MYA confirming species-level recognition as being most appropriate.

The molecular phylogeny of Ferchaud *et al.* (2012) found that *P. cathrynmatteoae kapelaensis subsp. nov.* diverged from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* about 0.7 MYA confirming subspecies-level recognition as being most appropriate for that taxon.

Distribution: Nominate *Pelias cathrynmatteoae sp. nov.* is confined to the Velebit Range, near the west coast of Croatia. The subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* occurs in the Kapela Range (part of the northern Dinaric Alps) and is believed to be confined to this area.

Etymology: *Pelias cathrynmatteoae sp. nov.* is named in honour of Cathryn Matteo of Hawthorn, Victoria, Australia in recognition of her services to herpetology spanning nearly 4 decades. She is also of southern European ancestry (Italian parents), reflecting the general area these vipers occur.

PELIAS CATHRYNMATTEOAE KAPALAENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:4D335234-33C8-4C70-81DB-26ACFA917617

Holotype: A specimen depicted in an image taken by Thomas Lindner in September 2017, collected from Velika Popina and posted in July 2022 on the website at: https://www.inaturalist.org/observations/126674083

Diagnosis: *Pelias cathrynmatteoae sp. nov.* from the Velebit Range, near the west coast of Croatia has until now been treated as a population of putative *P. ursinii* (Bonaparte, 1835), or alternatively the putative taxon *Pelias ursinii macrops* Mehely, 1911 herein treated as a subspecies of *Pelias rakosiensis* (Mehely, 1893), both of which it is proximally distributed with and morphologically similar to.

P. ursinii is herein restricted to central Italy and nearby parts of south-east France, while *P. rakosiensis* (as defined herein) is found in disjunct populations in Bosnia and Herzegovina, Montenegro, Albania, Macedonia, Hungary, Bulgaria, Moldavia and Romania.

The subspecies *Pelias rakosiensis macrops* (Mehely, 1911) is found in most parts of the Dinaric Alps within Bosnia and Herzegovina, as well as Montenegro and south to Albania.

In the Kapela Range (part of the northern Dinaric Alps), the subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* occurs, while nominate *P. cathrynmatteoae sp. nov.* is confined to the Velebit Range.

The following diagnostic information applies to adult male specimens unless otherwise stated.

Pelias cathrynmatteoae sp. nov. of both subspecies are readily separated from morphologically similar *P. ursinii* (all subspecies) and *P. rakosiensis* by the following unique combination of characters:

Tiny black barring on the posterior of the two upper labials below and behind the eye is thin and not always extending the length of the scale (upwards). Prominent blotches on either side of the flank of the body. Beige dorsum with dark brown to blackish-grey blotches, joined anteriorly and running down the midline, becoming broken posteriorly, this often forming the typical viper zig-zag configuration. On the midbody these blotches are large and circular, either merging or just broken, these becoming thinner posteriorly and elongate, becoming a zig-zag or broken zig zag.

Iris light orange.

The subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* is separated from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* by having prominent thin dark etching on the lower labials, versus not so in the nominate subspecies. The iris is also dull orange, versus bright orange. The supralabials below the eye are expanded to make the two suboculars flattened and reduced in overall size (as compared to the nominate subspecies).

In the nominate subspecies, the side blotches are usually mainly one colour only, versus obviously two colour in *P. cathrynmatteoae kapelaensis subsp. nov.*.

The nominate subspecies of *P. cathrynmatteoae sp. nov.* is depicted in life online at:

https://www.agefotostock.com/age/en/details-photo/meadow-viper-orsini-s-viper-Pelias-ursinii-lying-on-a-rock-croatia-velebit/BWI-BS265733

and

https://www.alamy.com/stock-photo-meadow-viper-orsinis-viper-Pelias-ursinii-on-the-feed-croatia-velebit-47915807.html

P. cathrynmatteoae kapelaensis subsp. nov. is depicted in life online at:

https://www.inaturalist.org/observations/126674083

The morphologically similar *P. ursinii* (Bonaparte, 1835) of the nominate subspecies from central Italy is separated from the preceding species by having heavy brown pigmentation in the iris, a beige to grey dorsal colouration (background colour) with some dark peppering. This being overlain with the dark viperine markings along the mid-dorsal line; thick dark bars or triangles at the posterior edge of the two upper labials below and behind the eye, these extending up to the top of the scale; these bars join below with equally thick dark bars on the lower labials and two over-sized suboculars. The side blotches are also prominent.

The two French subspecies of *P. ursinii* are readily separated from the nominate Italian form by having an obvious whitish-grey background colour. The side blotches are also fragmented in nature as opposed to being more-or-less squarish in the nominate subspecies.

The newly named subspecies *P. ursinii alpesdehautensis subsp. nov.* found east of the Durance River, France is separated from *P. ursinii wettsteini* Knoepffler and Sochurek, 1955 from west of the Durance River, France by having reduced blotching along the midline and narrow mid-dorsal blotches, meaning that on the mid-body these are broken up, whereas in *P. ursinii wettsteini* the same blotches are mostly broad and thick and mainly, but not always, joined to form a continuum.

Adult *P. ursinii alpesdehautensis subsp. nov.* also usually have yellowish flaring around the dark dorsal blotches, that runs into the grey background colouration, versus not so in adult *P. ursinii wettsteini.*
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and

https://www.inaturalist.org/observations/57009602

P. ursinii wettsteini is depicted in life online at:

https://www.inaturalist.org/observations/29586

and
https://www.inaturalist.org/observations/38419741
and

https://www.inaturalist.org/observations/122462979

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P. rakosiensis macrops is depicted in life online at:

https://www.inaturalist.org/observations/110557742

and

https://www.inaturalist.org/observations/24983835

P. rakosiensis rakosiensis Mehely, 1893 of the nominate subspecies from Hungary are characterised by relatively small and narrow blotches running down the midline of the dorsum, dark brown in the centres, blackish on the outer edged and with yellow flaring on the otherwise beige background. Side blotches appear as dark smudges.

The dark coloured underlying skin is particularly pronounced in this subspecies and more so than compared to all other subspecies as well as all forms of *P. ursinii.*

P. rakosiensis rakosiensis is depicted in life online at:

https://www.inaturalist.org/observations/42404735

P. rakosiensis moldavica (Nilson, Andren and Joger, 1993) is similar to *P. rakosiensis rakosiensis* as just described but has a dorsum with a whitish-grey background colour as opposed to beige.

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https://www.inaturalist.org/observations/118043961

and

https://www.inaturalist.org/observations/96766514

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It is further separated by having a white or pale brown venter, parietals frequently fragmented, generally fewer than 17 scale rows on posterior part of the body, 7 or 6 supralabials on each side, with the third always under the eye, posterior supralabials are noticeably smaller than the anterior ones, nasal plate often partly divided.

The two subspecies are separated as follows: There is no dark upper labial etching in the northern form being nominate *P. graeca graeca.* Southern specimens of the newly named subspecies *P. graeca vardusiaensis subsp. nov.* are separated from the nominate form by having obvious brown triangles rising from the lip in the 2 labials below and behind the eye. In the subspecies *P. graeca vardusiaensis subsp. nov.* the rear upper labials are only slightly smaller than the anterior and mid ones, versus significantly smaller in *P. graeca graeca.*

P. graeca of the nominate subspecies is depicted in life online at:

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and

https://www.inaturalist.org/observations/26665951

and in Nilson and Andren (1988) on pages 312 and 313.

P. graeca vardusiaensis subsp. nov. is depicted in life online at:
https://www.inaturalist.org/observations/26109978
All the preceding species and subspecies are separated from all other Vipers from Europe or elsewhere, by the following unique suite of characters: Scales on crown and snout are smooth or faintly keeled; nostril in a single or irregularly divided nasal, which is separated from the rostral by a naso-rostral; rostral usually in contact with a single apical scale; supraocular large and usually extending posteriorly beyond the vertical of the posterior border of the eye; frontal and parietal shields usually well developed; a single series of scales between the eye and the labials. Snout obtusely pointed, flat above, or with the canthus slightly raised but not obviously turned up or with any kind of appendage at the end; 6 to 9 upper labials, usually 7 or 8; 19 midbody scale rows, 120-142 ventrals; 18-41 subcaudals.

The molecular phylogeny of Ferchaud *et al.* (2012) found that *P. cathrynmatteoae sp. nov.* diverged from its nearest living relative, type *P. ursinii* just under 2 MYA confirming species-level recognition as being most appropriate.

The molecular phylogeny of Ferchaud *et al.* (2012) found that *P. cathrynmatteoae kapelaensis subsp. nov.* diverged from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* about 0.7 MYA confirming subspecies-level recognition as being most appropriate for that taxon.

Distribution: Nominate *Pelias cathrynmatteoae sp. nov.* is confined to the Velebit Range, near the west coast of Croatia. The subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* occurs in the Kapela Range (part of the northern Dinaric Alps) and is believed to be confined to this area.

Etymology: *Pelias cathrynmatteoae kapelaensis subsp. nov.* is named in reflection of where this subspecies occurs.

PELIAS URSINII ALPESDEHAUTENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:C2AD6FEF-5737-4837-ADB0-7133D0C2CD7B

Holotype: A preserved juvenile specimen at the Reptiles and Amphibians collection of the Museum national d'Histoire naturelle, Paris, France, specimen number MNHN RA 1978.457 collected from Lac de Lignins, at an elevation of 2100 m ASL, in Alpes-de-Haute-Provence, France.

This facility allows access to its holdings.

Paratypes: Three preserved juvenile specimens at the Reptiles and Amphibians collection of the Museum national d'Histoire naturelle, Paris, France, specimen numbers MNHN RA 1978.458, MNHN RA 1978.459 and MNHN RA 1978.460 all

collected from Lac de Lignins, at an elevation of 2100 m ASL, in Alpes-de-Haute-Provence, France.

Diagnosis: *P. ursinii* is herein restricted to central Italy and nearby parts of south-east France, while the closely related *P. rakosiensis* (as defined herein) is found in disjunct populations in Bosnia and Herzegovina, Montenegro, Albania, Macedonia, Hungary, Bulgaria, Moldavia and Romania.

Pelias cathrynmatteoae sp. nov. from the Velebit Range, near the west coast of Croatia has until now been treated as a population of putative *P. ursinii* (Bonaparte, 1835), or alternatively the putative taxon *Pelias ursinii macrops* Mehely, 1911 herein treated as a subspecies of *Pelias rakosiensis* (Mehely, 1893), both of which it is proximally distributed with and morphologically similar to.

Pelias cathrynmatteoae sp. nov. is morphologically most similar to *P. ursinii* and also most closely related to it, having diverged just under 2 MYA accorrding to Ferchaud *et al*. (2012).

The subspecies *Pelias rakosiensis macrops* (Mehely, 1911) is found in most parts of the Dinaric Alps within Bosnia and Herzegovina, as well as Montenegro and south to Albania.

In the Kapela Range (part of the northern Dinaric Alps), the subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* occurs, while nominate *P. cathrynmatteoae sp. nov.* is confined to the Velebit Range.

The following diagnostic information applies to adult male specimens unless otherwise stated.

Pelias cathrynmatteoae sp. nov. of both subspecies are readily separated from morphologically similar *P. ursinii* (all subspecies) and *P. rakosiensis* by the following unique combination of characters:

Tiny black barring on the posterior of the two upper labials below and behind the eye is thin and not always extending the length of the scale (upwards). Prominent blotches on either side of the flank of the body. Beige dorsum with dark brown to blackish-grey blotches, joined anteriorly and running down the midline, becoming broken posteriorly, this often forming the typical viper zig-zag configuration. On the midbody these blotches are large and circular, either merging or just broken, these becoming thinner posteriorly and elongate, becoming a zig-zag or broken zig zag.

Iris light orange.

The subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* is separated from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* by having prominent thin dark etching on the lower labials, versus not so in the nominate subspecies. The iris is also dull orange, versus bright orange. The supralabials below the eye are expanded to make the two suboculars flattened and reduced in overall size (as compared to the nominate subspecies).

In the nominate subspecies, the side blotches are usually mainly one colour only, versus obviously two colour in *P. cathrynmatteoae kapelaensis subsp. nov.*.

The nominate subspecies of *P. cathrynmatteoae sp. nov.* is depicted in life online at:

https://www.agefotostock.com/age/en/details-photo/meadow-viper-orsini-s-viper-Pelias-ursinii-lying-on-a-rock-croatia-velebit/BWI-BS265733

and

https://www.alamy.com/stock-photo-meadow-viper-orsinis-viper-Pelias-ursinii-on-the-feed-croatia-velebit-47915807.html

P. cathrynmatteoae kapelaensis subsp. nov. is depicted in life online at:

https://www.inaturalist.org/observations/126674083

The morphologically similar *P. ursinii* (Bonaparte, 1835) of the nominate subspecies from central Italy is separated from the preceding species by having heavy brown pigmentation in the iris, a beige to grey dorsal colouration (background colour) with some dark peppering. This being overlain with the dark viperine markings along the mid-dorsal line; thick dark bars or triangles at the posterior edge of the two upper labials below and behind the eye, these extending up to the top of the scale; these bars join below with equally thick dark bars on the lower labials and two over-sized suboculars. The side blotches are also prominent.

The two French subspecies of *P. ursinii* are readily separated from the nominate Italian form as described above, by having an obvious whitish-grey background colour. The side blotches are also fragmented in nature as opposed to being more-or-less squarish in the nominate subspecies.

The newly named subspecies *P. ursinii alpesdehautensis subsp. nov.* found east of the Durance River, France is separated from *P. ursinii wettsteini* Knoepffler and Sochurek, 1955 from west of the Durance River, France by having reduced blotching along the midline and narrow mid-dorsal blotches, meaning that on the mid-body these are broken up, whereas in *P. ursinii wettsteini* the same blotches are mostly broad and thick and mainly, but not always, joined to form a continuum.

Adult *P. ursinii alpesdehautensis subsp. nov.* also usually have yellowish flaring around the dark dorsal blotches, that runs into the grey background colouration, versus not so in adult *P. ursinii wettsteini.*
There is sometimes brown flaring of the blotches in adult *P. ursinii wettsteini.*
P. ursinii alpesdehautensis subsp. nov. is depicted in life online at:
https://www.inaturalist.org/observations/109925430

and

https://www.inaturalist.org/observations/57009602

P. ursinii wettsteini is depicted in life online at:

https://www.inaturalist.org/observations/29586

and
https://www.inaturalist.org/observations/38419741
and

https://www.inaturalist.org/observations/122462979

Pelias rakosiensis (Mehely, 1893) of all subspecies are separated from the two preceding species by having side blotches that are either indistinct or absent, or otherwise faded, and no prominent etching on the two upper labials below and behind the eye. Dorsum is usually beige or with a light brownish rinse through it, rather than grey and the mid-dorsal blotches are brown to dark brown, rather than black. Blotches on the mid-line of the upper and mid body are more triangular than circular as seen in both *P. cathrynmatteoae sp. nov.* and *P. ursinii.*

P. rakosiensis macrops is depicted in life online at:

https://www.inaturalist.org/observations/110557742

and

https://www.inaturalist.org/observations/24983835

P. rakosiensis rakosiensis Mehely, 1893 of the nominate subspecies from Hungary are characterised by relatively small and narrow blotches running down the midline of the dorsum, dark brown in the centres, blackish on the outer edged and with yellow flaring on the otherwise beige background. Side blotches appear as dark smudges.

The dark coloured underlying skin is particularly pronounced in this subspecies and more so than compared to all other subspecies as well as all forms of *P. ursinii.*

P. rakosiensis rakosiensis is depicted in life online at:

https://www.inaturalist.org/observations/42404735

P. rakosiensis moldavica (Nilson, Andren and Joger, 1993) is similar to *P. rakosiensis rakosiensis* as just described but has a dorsum with a whitish-grey background colour as opposed to beige.

P. rakosiensis moldavica is depicted in life online at:

https://www.inaturalist.org/observations/118043961

and

https://www.inaturalist.org/observations/96766514

The morphologically similar species, *P. graeca* Nilson and Andren, 1988 is separated from all the preceding species by having a purplish-brown iris and by subcaudal counts. In males it is 20-27 and females is 18-21. This contrasts with 27-41 in males and 20-32 in the other preceding species.

It is further separated by having a white or pale brown venter, parietals frequently fragmented, generally fewer than 17 scale rows on posterior part of the body, 7 or 6 supralabials on each side, with the third always under the eye, posterior supralabials are noticeably smaller than the anterior ones, nasal plate often partly divided.

The two subspecies are separated as follows: There is no dark upper labial etching in the northern form being nominate *P. graeca graeca.* Southern specimens of the newly named subspecies *P. graeca vardusiaensis subsp. nov.* are separated from the nominate form by having obvious brown triangles rising from the lip in the 2 labials below and behind the eye. In the subspecies *P. graeca vardusiaensis subsp. nov.* the rear upper labials are only slightly smaller than the anterior and mid ones, versus significantly smaller in *P. graeca graeca.*

P. graeca of the nominate subspecies is depicted in life online at:

https://www.inaturalist.org/observations/20192192

and

https://www.inaturalist.org/observations/26665951

and in Nilson and Andren (1988) on pages 312 and 313.

P. graeca vardusiaensis subsp. nov. is depicted in life online at:
https://www.inaturalist.org/observations/26109978
All the preceding species and subspecies are separated from all other Vipers from Europe or elsewhere, by the following unique suite of characters: Scales on crown and snout are smooth or faintly keeled; nostril in a single or irregularly divided nasal, which is separated from the rostral by a naso-rostral; rostral usually in contact with a single apical scale; supraocular large and usually extending posteriorly beyond the vertical of the posterior border of the eye; frontal and parietal shields usually well developed; a single series of scales between the eye and the labials. Snout obtusely pointed, flat above, or with the canthus slightly raised but not obviously turned up or with any kind of appendage at the end; 6 to 9 upper labials, usually 7 or 8; 19 midbody scale rows, 120-142 ventrals; 18-41 subcaudals.

The molecular phylogeny of Ferchaud *et al.* (2012) found that *P. cathrynmatteoae sp. nov.* diverged from its nearest living relative, type *P. ursinii* just under 2 MYA confirming species-level recognition as being most appropriate.

The molecular phylogeny of Ferchaud *et al.* (2012) found that *P. cathrynmatteoae kapelaensis subsp. nov.* diverged from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* about 0.7 MYA confirming subspecies-level recognition as being most appropriate for that taxon.

The molecular phylogeny of Ferchaud *et al.* (2012), following on from Ferchaud *et al.* (2011), found that the two French populations of *P. ursiniii* diverged from one another about 0.5 MYA and about 0.6 MYA from the nominate Italian form, confirming subspecies-level recognition as being most appropriate for these taxa.

Distribution: The newly named subspecies *P. ursinii alpesdehautensis subsp. nov.* is found east of the Durance River, France and within France, while *P. ursinii wettsteini* Knoepffler and Sochurek, 1955 is found in a small area generally west of the Durance River, France.

Etymology: The newly named subspecies *P. ursinii alpesdehautensis subsp. nov.* is named in reflection of the type locality and where it occurs.

PELIAS GRAECA VARDOUSIAENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:A164BD7F-F600-4D66-8D1E-B12A601FB25D

Holotype: A specimen collected from about 15 km north-west of Mount Giona, Greece, depicted in an image posted online by Balázs Bozóki at:
https://www.inaturalist.org/observations/26109978

Diagnosis: *Pelias graeca* Nilson and Andren, 1988 is separated from all other species and subspecies in the *Pelias ursinii* Bonaparte, 1835 species complex by having a purplish-brown iris and by subcaudal counts. In males it is 20-27 and females is 18-21. This contrasts with 27-41 in males and 20-32 in all the other species.

It is further separated by having a white or pale brown venter, parietals frequently fragmented, generally fewer than 17 scale rows on the posterior part of the body, 7 or 6 supralabials on each side, with the third always under the eye, posterior supralabials are noticeably smaller than the anterior ones, nasal plate often partly divided.

The two subspecies are separated as follows: There is no dark upper labial etching in the northern form being nominate *P. graeca graeca.* Southern specimens of the newly named subspecies *P. graeca vardusiaensis subsp. nov.* are separated from the nominate form by having obvious brown triangles rising from the lip in the 2 labials below and behind the eye. In the subspecies *P. graeca vardusiaensis subsp. nov.* the rear upper labials are only slightly smaller than the anterior and mid ones (being the largest), versus significantly smaller in *P. graeca graeca.*

P. graeca of the nominate subspecies is depicted in life online at:

https://www.inaturalist.org/observations/20192192

and

https://www.inaturalist.org/observations/26665951

and in Nilson and Andren (1988) on pages 312 and 313.

P. graeca vardusiaensis subsp. nov. is depicted in life online at:
https://www.inaturalist.org/observations/26109978
P. ursinii the species-level taxon to which *P. graeca* was originally assigned, is herein restricted to central Italy and nearby parts of south-east France, while the closely related *P. rakosiensis* (as defined herein) is found in disjunct populations in Bosnia and Herzegovina, Montenegro, Albania, Macedonia, Hungary, Bulgaria, Moldavia and Romania.

Pelias cathrynmatteoae sp. nov. from the Velebit Range, near the west coast of Croatia has until now been treated as a population of putative *P. ursinii* (Bonaparte, 1835), or alternatively the putative taxon *Pelias ursinii macrops* Mehely, 1911 herein treated as a subspecies of *Pelias rakosiensis* (Mehely, 1893), both of which it is proximally distributed with and morphologically similar to.

Pelias cathrynmatteoae sp. nov. is morphologically most similar to *P. ursinii* and also most closely related to it, having diverged just under 2 MYA accorrding to Ferchaud *et al*. (2012).

The subspecies *Pelias rakosiensis macrops* (Mehely, 1911) is found in most parts of the Dinaric Alps within Bosnia and Herzegovina, as well as Montenegro and south to Albania.

In the Kapela Range (part of the northern Dinaric Alps), the subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* occurs, while nominate *P. cathrynmatteoae sp. nov.* is confined to the Velebit Range.

The following diagnostic information applies to adult male specimens unless otherwise stated.

Pelias cathrynmatteoae sp. nov. of both subspecies are readily separated from morphologically similar *P. ursinii* (all subspecies) and *P. rakosiensis* by the following unique combination of characters:

Tiny black barring on the posterior of the two upper labials below

and behind the eye is thin and not always extending the length of the scale (upwards). Prominent blotches on either side of the flank of the body. Beige dorsum with dark brown to blackish-grey blotches, joined anteriorly and running down the midline, becoming broken posteriorly, this often forming the typical viper zig-zag configuration. On the midbody these blotches are large and circular, either merging or just broken, these becoming thinner posteriorly and elongate, becoming a zig-zag or broken zig zag.

Iris light orange.

The subspecies *Pelias cathrynmatteoae kapelaensis subsp. nov.* is separated from the nominate subspecies *P. cathrynmatteoae cathrynmatteoae subsp. nov.* by having prominent thin dark etching on the lower labials, versus not so in the nominate subspecies. The iris is also dull orange, versus bright orange. The supralabials below the eye are expanded to make the two suboculars flattened and reduced in overall size (as compared to the nominate subspecies).

In the nominate subspecies, the side blotches are usually mainly one colour only, versus obviously two colour in *P. cathrynmatteoae kapelaensis subsp. nov.*.

The nominate subspecies of *P. cathrynmatteoae sp. nov.* is depicted in life online at:

https://www.agefotostock.com/age/en/details-photo/meadow-viper-orsini-s-viper-Pelias-ursinii-lying-on-a-rock-croatia-velebit/BWI-BS265733

and

https://www.alamy.com/stock-photo-meadow-viper-orsinis-viper-Pelias-ursinii-on-the-feed-croatia-velebit-47915807.html

P. cathrynmatteoae kapelaensis subsp. nov. is depicted in life online at:

https://www.inaturalist.org/observations/126674083

The morphologically similar *P. ursinii* (Bonaparte, 1835) of the nominate subspecies from central Italy is separated from the preceding species by having heavy brown pigmentation in the iris, a beige to grey dorsal colouration (background colour) with some dark peppering. This being overlain with the dark viperine markings along the mid-dorsal line; thick dark bars or triangles at the posterior edge of the two upper labials below and behind the eye, these extending up to the top of the scale; these bars join below with equally thick dark bars on the lower labials and two over-sized suboculars. The side blotches are also prominent.

The two French subspecies of *P. ursinii* are readily separated from the nominate Italian form as described above, by having an obvious whitish-grey background colour. The side blotches are also fragmented in nature as opposed to being more-or-less squarish in the nominate subspecies.

The newly named subspecies *P. ursinii alpesdehautensis subsp. nov.* found east of the Durance River, France is separated from *P. ursinii wettsteini* Knoepffler and Sochurek, 1955 from west of the Durance River, France by having reduced blotching along the midline and narrow mid-dorsal blotches, meaning that on the mid-body these are broken up, whereas in *P. ursinii wettsteini* the same blotches are mostly broad and thick and mainly, but not always, joined to form a continuum.

Adult *P. ursinii alpesdehautensis subsp. nov.* also usually have yellowish flaring around the dark dorsal blotches, that runs into the grey background colouration, versus not so in adult *P. ursinii wettsteini.*
There is sometimes brown flaring of the blotches in adult *P. ursinii wettsteini.*
P. ursinii alpesdehautensis subsp. nov. is depicted in life online at:
https://www.inaturalist.org/observations/109925430

and

https://www.inaturalist.org/observations/57009602

P. ursinii wettsteini is depicted in life online at:

https://www.inaturalist.org/observations/29586

and
https://www.inaturalist.org/observations/38419741
and

https://www.inaturalist.org/observations/122462979

Pelias rakosiensis (Mehely, 1893) of all subspecies are separated from the two preceding species by having side blotches that are either indistinct or absent, or otherwise faded, and no prominent etching on the two upper labials below and behind the eye. Dorsum is usually beige or with a light brownish rinse through it, rather than grey and the mid-dorsal blotches are brown to dark brown, rather than black. Blotches on the mid-line of the upper and mid body are more triangular than circular as seen in both *P. cathrynmatteoae sp. nov.* and *P. ursinii.*

P. rakosiensis macrops is depicted in life online at:

https://www.inaturalist.org/observations/110557742

and

https://www.inaturalist.org/observations/24983835

P. rakosiensis rakosiensis Mehely, 1893 of the nominate subspecies from Hungary are characterised by relatively small and narrow blotches running down the midline of the dorsum, dark brown in the centres, blackish on the outer edged and with yellow flaring on the otherwise beige background. Side blotches appear as dark smudges.

The dark coloured underlying skin is particularly pronounced in this subspecies and more so than compared to all other subspecies as well as all forms of *P. ursinii.*

P. rakosiensis rakosiensis is depicted in life online at:

https://www.inaturalist.org/observations/42404735

P. rakosiensis moldavica (Nilson, Andren and Joger, 1993) is similar to *P. rakosiensis rakosiensis* as just described but has a dorsum with a whitish-grey background colour as opposed to beige.

P. rakosiensis moldavica is depicted in life online at:

https://www.inaturalist.org/observations/118043961

and

https://www.inaturalist.org/observations/96766514

All the preceding species and subspecies are separated from all other Vipers from Europe or elsewhere, by the following unique suite of characters: Scales on crown and snout are smooth or faintly keeled; nostril in a single or irregularly divided nasal, which is separated from the rostral by a naso-rostral; rostral usually in contact with a single apical scale; supraocular large and usually extending posteriorly beyond the vertical of the posterior border of the eye; frontal and parietal shields usually well developed; a single series of scales between the eye and the labials. Snout obtusely pointed, flat above, or with the canthus slightly raised but not obviously turned up or with any kind of appendage at the end; 6 to 9 upper labials, usually 7 or 8; 19 midbody scale rows, 120-142 ventrals; 18-41 subcaudals.

There has not yet been a molecular analysis of specimens of the new subspecies *P. graeca vardusiaensis subsp. nov.* to compare with the nominate form.

Distribution: The subspecies is believed to be restricted to the area of Vardousia, southern Greece.

Etymology: The subspecies is named in reflection of where it occurs in Greece.

CONSERVATION

The four newly named Viper taxa are all range restricted species or subspecies and self-evidently should be managed as separate conservation units.
While their known habitats are largely within relatively undisturbed and protected habitats, direct human pressures and human created problems and risks remain and likely to increase into the future as the world human population increases and

demand for resources from currently less intensively utilized areas is likely to increase.

In recent years, seemingly secure populations of vertebrate species have declined and sometimes expired, often quickly and without any immediately obvious reason.

With this in mind, it makes sense that specimens of each species of subspecies of European viper should be brought into captivity and bred as an insurance against some unforseen calamity in wild populations.

Because of the popularity of snakes and herpetoculture as a hobby, the most expedient way to solve the problem is to allow private individuals to bring specimens into captivity and to trade them legally.

The small adult size of the relevant species (average 50 cm total length in adults) does not make them a popular exhibit in large government-owned zoos and commercially oriented fauna parks, but does make them highly suitable for hobbyists to keep in private homes.

A captive population of each relevant taxon named herein could be maintained by hobbyists at no costs to taxpayers and enabling government conservation dollars to be spent on other pressing needs, for which private citizen involvement is not a viable option.

The relevant comments of Cogger (2014), Cotton (2014), Hawkeswood (2021), Hoser (1989, 1991, 1993, 1996, 2001a-b, 2007, 2009, 2012a-b, 2013, 2015a-f, 2017, 2019a-b), ICZN (1991, 2001, 2021) and Wellington (2015) all apply with respect of these three taxa.

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CONFLICT OF INTEREST - NONE.

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Europe gets new viper species: *Vipera ammodytes* (Linnaeus, 1758) *sensu lato* formally divided!

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ABSTRACT

The well-known European Long-nosed Viper, *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, has been subject of taxonomic splitting many times over the past 250 years.

However only one other species in the complex is generally recognized, that being *V. transcaucasiana* Boulenger, 1913.

Recent molecular studies have shown there to be at least 12 lineages within these two putative species with divergences in excess of 2 MYA.

Morphologically divergent populations match these lineages and so all are herein recognized as full species.

Seven species are recognized using available names. Other available names as listed by McDiarmid *et al.* (1999) are all synonyms of the other seven species.

The other five species are formally described and named for the first time in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999) as amended since (ICZN 2012).

Another eight morphologically divergent populations with deep molecular divergences are also conservatively named herein as new subspecies.

With all 12 species and the eight new subspecies subject to significant persecution by humans across their ranges, it is important that they each be recognized as separate taxonomic entities immediately and before any one of them becomes extinct through the misconception they are merely a part of a common and widespread species as occurred in the example cited by Hoser (2019a, 2019b).

With a divergence from all other vipers estimated to be more than 15 MYA (Freitas *et al*. 2020), a new genus name for the group *Longumnaribussuis gen. nov*. is formally proposed, with all newly named taxa also placed within this new genus.

Two earlier proposed generic names do not appear to be available.

Keywords: Viper; Europe; long-nosed viper; Greece; Turkey; Peloponnisos; Cyclades; *Vipera*; *ammodytes*; *meridionalis*; *steindachneri*; *connectons*; *montandoni*; *transcaucasiana*; *buchholzi;* new genus; *longumnaribussuis*; new species; *montenegroensis*; *epirusensis*; *maxhoseri*; *mariolisi*; *shireenhoserae*; new subspecies; *eviaensis*; *lefkadaensis*; *sirosensis*; *mykonosensis*; *androsensis*; *naxosensis*; *sikinosensis*; *koufonissiensis.*

INTRODUCTION

The well-known European Long-nosed Viper, *Vipera ammodytes* (Linnaeus, 1758), has been subject of taxonomic splitting many times over the past 250 years.

However only one other species in the complex is generally recognized, that being *V. transcaucasiana* Boulenger, 1913.

Recent molecular studies including those of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020) have all shown there to be at least 12 lineages within these two putative species with divergences in excess of 2 MYA.

These populations appear to be allopatric and while some have been morphologically defined as either species or subspecies in the past, this is certainly not the case for all.

Because it appeared that the morphologically divergent populations matched some or all of these lineages it was decided to audit *V. ammodytes* (Linnaeus, 1758) *sensu lato* to arrive at a taxonomy that reflects reality both in terms of lineages to be recognized as distinct species and the correct ICZN names that can be applied to them.

No one else had in the past 5 years indicated an intention to review the complex and name species and so I had no hesitation in taking up the task.

The urgency was increased somewhat in view of the ongoing persecution of vipers across Europe, especially in Catholic and Orthodox regions where snakes are viewed as being associated with "The Devil" and killed on sight.

If as expected, a sometimes wide-ranging species became a group of range restricted taxa, one or more of these may in fact be of immediate conservation concern.

Saving them would of course also hinge on them being properly identified and named and differentiated from any other potentially more widespread form, or one that may be abundant in another area.

MATERIALS AND METHODS

All relevant literature was reviewed relevant to *Vipera ammodytes* (Linnaeus, 1758) *sensu lato* to assist in determining if any of the putative taxa identified in molecular studies as divergent, was in fact so and/or could be separated from others on a morphological basis.

In tandem with this was a check of all previously published descriptions applicable to the species group to determine available names and to which specific taxon they applied to.

Simultaneously, specimens were examined from across the range of the species complex, including live, dead, preserved and from photos of specimens with good locality data.

Literature relevant to the taxonomy, nomenclature and final conclusions within this paper included Akkaya and Ugurtas (2012), Anastasakis and Dermitzakis (1990), Andelkovic *et al.* (2021), Bedragia (1882), Beerli *et al*. (1996), Beschov (1977), Beshkov and Nanev (2006), Beutler and Fror (1980), Biella and Blättler (1989), Billing *et al.* (1990), Bintanja *et al.* (2005), Bird (1935), Bodson (2009), Boettger (1880, 1888), Bohlmann *et al*. (1981), Bolkay (1919, 1920, 1924, 1930), Bonaparte (1835), Boulenger (1896, 1903, 1904, 1913a-b), Brammah *et al.* (2010), Bringsøe (2019), Broggi (1996), Bruno (1968), Buchholz (1955), Buchholz and Schultze-Westrum (1964), Buresch and Zonkov (1934), Buseke (1982), Buttle (1993), Cabela and Tiedemann (1985), Cattaneo (1997, 2001, 2010, 2021, 2022), Cattaneo and Cattaneo (2016), Chondropoulos (1989), Clark (1965, 1967, 1968, 1969), Cogălniceanu *et al.* (2013), Covaciu-Marcov *et al.* (2006), Covaciu-Marcov *et al*. (2009), Cox *et al.* (2006), Čubrić and Crnobrnja-Isailović (2017), Crnobrnja-Isailovic *et al*. (2007), Dalla Torre (1912), Derjugin (1901), Diesener (1979, 1981), Dimitropoulos and Ioannidis (2002), Dunaev and Orlova (2003), Dyugmedzhiev (2020), Dyugmedzhiev *et al*. (2019, 2021a-b), Ebner (1912), Erber (1867), Faoro (1986, 1987), Ferchaud *et al.* (2012), Fielder (1841), Foufopoulos *et al.* (2011), Freitas *et al.* (2020), Gaki-Papanastassiou *et al*. (2010), Gandini (2021), Garcia-Castellanos *et al.* (2009), Garrigues *et al*. (2005), Gebhart (2020), Gemel *et al*. (2019), Gestel (1983), Göçmen *et al.* (2014), Golay *et al.* (1993), Greene (1997), Gruber (2009), Gruber and Fuchs (1977), Gulden (1988), Gvozdenovic and Ikovic (2022), Gvoždík *et al.* (2010), Hawkeswood (2021), Hermann *et al*. (1992), Hewitt (1999), Hurston *et al*. (2009), Jablonski (2011), Janssen (1981), Kabisch (1966), Kabisch and Belter (1968), Kabisch and Engelhard (1964), Kapsimalis *et al*. (2009), Kasapidis *et al*. (2005), Kindler *et al.* (2013), Kopstein and Wettstein (1921), Kornilios *et al*. (2014), Kougioumoutzis *et al*. (2014), Krecsák (2007, 2008), Kutrup (1999, 2000), Kyriazi *et al*. (2012), Kwet (2010), Kwet and Trapp (2014a-b), Lakušić *et al.* (2021), Laurenti (1768), Legakis and Maragou (2009), Linnaeus (1758), Lotze (1973), Luiselli (1996), Lykousis (2009), Lymberakis and Poulakakis (2010), Mallow *et al*. (2003), Marktanner-Turneretscher (1904), Mayer *et al.* (2000), McDiarmid *et al.* (1999), Mebert *et al.* (2014, 2015), Melani (2005), Mertens and Müller (1928), Meuth (1913), Meyer (1985), Mojsisovics (1889), Mulder (2017), Naulleau (1975), Nilson *et al*. (1988, 1999a-c), Obermayer (1967), Obst (1983), Pafilis (2010), Perissoratis and Conispoliatis (2003), Petit *et al*. (2003), Pezdirc *et al*. (2013), Phelps (2010), Pichler (2014), Plessas (2002), Plettenberg-Lang (2020), Polovic and Cadenovic (2014), Poulakakis *et al.* (2003, 2015), Reuss (1927, 1933), Ride *et al*. (1999), Ripa (1983), Rödel and Bussmann (1990), Rohling *et al*. (2014), Roussos (2013, 2014), Roussos and Densmore (2013), Sagonas *et al*. (2014), Saint-Girons (1978), Sajovic (1914), Schlüter (2003, 2006), Schmidt *et al*. (2020), Schwarz (1936), Schweiger (1992a-b, 2009a-c, 2012, 2013). Schweizer (1941), Shine and Madsen (1984), Sindaco *et al.* (2013), Smith (2016), Sochurek (1976), Sos (2008), Stoev (2000), Strachinis and Aravanis (2017), Strauch (1868), Stümpel and Hahn (2001), Thanou *et al*. (2014), Thieme (1986), Thomas (1969), Tok and Kumlutaş (1996), Tomović (2006), Tomović and Džukić (2003), Tomović *et al*. (2002), Torstrom *et al*. (2014), Tóth *et al*. (2002), Trapp (2007, 2014), Trutnau (1975), Tuniyev *et al*. (2014, 2019), Ursenbacher *et al.* (2006, 2008), Veith (1991), Wallach *et al.* (2014), Weima (2009a-b, 2011a-b, 2013, 2014), Werner (1899, 1904, 1930, 1935, 1938a, 1938b), Wettstein (1953), Wirth (2010, 2012a-b), Wöss (1989), Wütschert (1984), Zadravec and Koren (2017), Žagar *et al*. (2014), Zauner (2021), Zinenko (2015) and sources cited therein.

RESULTS

Seven species are recognized using available names. Other available names as listed by McDiarmid *et al.* (1999) are all synonyms of the other seven species.

The other five species are all morphologically separable from one another and therefore are formally described and named for the first time in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al*. 1999) as amended since (ICZN 2012).

Eight divergent and mainly insular populations clearly evolving separately, with deep molecular divergences are also conservatively formally named herein as new subspecies.

Based on divergence times estimated by Roussos (2015), being well over 2 MYA for each taxon, each of these and perhaps some other still unnamed insular forms should in fact be treated as full species.

Certainly this remains a possibility for the future.

My hesitation in naming the eight relevant forms as full species as opposed to subspecies as done within this paper, stems from a belief that Roussos (2015) may have over-estimated some of the divergence times.

The mtDNA divergence he reported for the north and south Cyclades populations of putative *V. ammodytes* indicated subspecies-level divergence and less than his published estimates in his Fig. 4.8 of 5.33 MYA, based on sea depth evidence, supported by the concept of the dating of the Messinian Salinity Crisis, Zanclean flood and relevant sea depths between the islands, meaning permanent inundation as a barrier ever since.

In light of the molecular findings of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020) and others, indicating a divergence of the *V. ammodytes* complex from nearest relatives of more than 15 MYA, it is self evident that these snakes should be placed in a separate genus to other *Vipera* Laurenti, 1768 (type species *Vipera francisci redi* Laurenti, 1768 (= *Vipera aspis* (Linnaeus, 1758)).

Two genus-level names have been previously proposed for this group, however neither is available.

Rhinaspis Bonaparte, 1934 is a junior homonym for *Rhinaspis* Perty, 1830 (Insecta).

The name *Teleovipera* Reuss, 1927, is also not available.

Krecsák (2007) noted:

"Teleovipera *Reuss, 1927c: 125. [Published as a synonym for* Vipera sensu *Reuss (i.e.* Vipera *Gronovius, 1763 non* Vipera *Laurenti, 1768), thus* nomen illegitimum*, according to Art. 11.6. of the Code (ICZN 1999).*]"

In light of no available names, members of this species complex are herein assigned to the new genus *Longumnaribussuis gen. nov.*.

This in effect means that all use of the genus name "*Vipera*" or the abbreviated "*V.*" relevant to species in the "*V. ammodytes* complex" should be taken as from this time on being in the new genus *Longumnaribussuis gen. nov.*.

(Species and subspecies descriptions in this paper will treat all as within *Longumnaribussuis gen. nov.*).

In light of the molecular findings of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020), the biogeographical evidence based on distribution and barriers caused by sea levels and or broad topography and habitat constraints, including in terms of the past several million years and morphological differences between relevant specimens, the key findings are summarised below.

INSERTED NOTE / TAXONOMIC VANDALISM

While this paper was being peer reviewed in 2021, Augusto Cattaneo, of Italy, evidently aware that I was preparing a paper on this group of vipers, rushed out and published a poorly constructed paper formally naming a taxon that was to be named in this paper from the Cyclades in Greece (Cattaneo 2021).

I note that his concept of that taxon and other Cyclades populations does not match the species and subspecies concepts within this paper or for that matter even remotely reflect the biological reality of the said snakes!

Notwithstanding the moral issues involved, I note that his name is published in the sense of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999) and is therefore available for zoological nomenclature.

It must therefore be used in priority to any name I had intended to propose in accordance with the Code rule of priority (Article 23, Principle of Priority), so my proposed name for that taxon has been scrubbed and erased from this paper, and the paper rewritten accordingly (with quite some difficulty, due to the changes required in a number of descriptions), as it would be wasteful to unnecessarily create a junior synonym.

The so called "Kaiser *et al*. (2013)" edict directing names to be overwritten at whim, especially if the publishing author is not a member of your own "cohort" is not ICZN supported or allowed (ICZN 2021) and is illegal under copyright laws including for example by being in breach of the Australian Copyright Act 1968, Moral Rights Provisions, the relevant parts being within Sections 36, 115, 189-190, 193-195, in particular Sections 195AI (2) and 195AJ (a-b) and 195 AQ(2)).

The ICZN made a scathing ruling against Kaiser *et al*. (2013) and their later incarnation of that manifesto, known as "Rhodin *et al*. 2015" in 2021 (ICZN 2021).

Cattaneo's taxon, identified as "*Vipera ammodytes buchholzi*" with a type locality of Antiparos Island, was restricted to populations from Antiparos and Paros islands in the Cyclades only.

In this paper and relying on the molecular evidence of Roussos (2015), that taxon (as a species) is taken to include all Cyclades specimens from islands between Andros in the north and Sikinos and Ios in the south and recognized herein as a full species.

In turn that species is broken up into seven subspecies, with three from the northern Cyclades and four from the central and southern islands, including the nominate form of "*Vipera ammodytes buchholzi*".

My originally intended nomen for the Antiparos form has been scrubbed from this paper.

This matter was complicated further in that the island race that was named by Cattaneo was in fact to be a subspecies of a taxon named from another island in the Cyclades, with all relevant Cyclades forms being named as a subspecies of a pan Cyclades species.

Hence a substantial rewrite of the relevant parts of the paper had to be undertaken prior to final publication.

The nominate form for the Cyclades as originally written into this paper has in turn been made a subspecies of the form described as "*Vipera ammodytes buchholzi*".

Furthermore "*Vipera ammodytes buchholzi*" as described by Cattaneo was taken as being a taxon confined to Antiparos and Paros islands only.

This situation appears contrary to the morphological and genetic evidence and so as a subspecies it is revised to be the taxon from Antiparos and Despotiko islands in this paper.

The snakes from Paros are herein included within the subspecies *L. buchholzi naxosensis subsp. nov.*, also occurring on the islands of Naxos, Iraklia and Ios islands in the southern Cyclades (type locality Naxos).

I might also note that I was unable to source any hard copies of Cattaneo (2021), meaning that it may only be an online paper.

The unavailability of hard copies was confirmed by way of enquiries I made online and a lack of response from an email sent to the publisher of the journal.

The doi listed in the online paper was:
DOI: https://doi.org/10.5281/zenodo.5713465

That in turn resolved to:
https://zenodo.org/record/5713465#.Y7TIIH1Bypo

On that webpage (saved) was the following information:

"*Publication date:*
November 25, 2021
DOI:
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Keyword(s):
Cicladi, Sporadi settentrionali, morfotipi, nuova sottospecie
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Version 1 10.5281/zenodo.5713465
Cite as
AUGUSTO CATTANEO. (2021). VARIABILITÀ DI VIPERA AMMODYTES (LINNAEUS, 1758) (Reptilia Viperidae) IN ALCUNE ISOLE EGEE, CON DESCRIZIONE DI VIPERA AMMODYTES BUCHHOLZI SUBSP. NOVA. https://doi.org/10.5281/zenodo.5713465"

There was no reference to hard copy paper, meaning it may well have only been published as a pdf.

The 2012 "*Amendment of Articles 8, 9, 10, 21 and 78 of the* International Code of Zoological Nomenclature *to expand and refine methods of publication*" (ICZN 2012), stated:

"*The International Commission on Zoological Nomenclature has voted in favour of a revised version of the amendment to the* International Code of Zoological Nomenclature *that was proposed in 2008. The purpose of the amendment is to expand and refine the methods of publication allowed by the Code, particularly in relation to electronic publication. The amendment establishes an Official Register of Zoological Nomenclature (with ZooBank as its online version), allows electronic publication after 2011 under certain conditions, and disallows publication on optical discs after 2012. The requirements for electronic publications are that the work be registered in ZooBank before it is published, that the work itself state the date of publication and contain evidence that registration has occurred, and that the ZooBank registration state both the name of an electronic archive intended to preserve the work and the ISSN or ISBN associated with the work*."

The pdf version on Cattaneo (2021) does not have any Zoobank registration details in that paper.

This means that if the paper was only published in 2021 as a pdf, then the name within it is unavailable for zoological nomenclature.

That would in turn make "*Vipera ammodytes buchholzi*" treated herein as "*Vipera buchholzi*" an unavailable name and the relevant taxon would then be *Vipera sirosensis sp. nov.*" (herein placed within *Longumnaribussuis gen. nov.*), with all relevant subspecies being of that taxon (*L. sirosensis sp. nov.*). In turn the subspecies as defined herein as "*L. buchholzi buchholzi*" would in fact be an undescribed or unnamed subspecies of *L. sirosensis sp. nov.*.

Rather than progress this paper on the basis Cattaneo (2021) was published only online, I have given the benefit of the doubt to Cattaneo so as to avoid the potential creation of an unnecessary junior synonym.

However the exact question of publication status of Cattaneo (2021) will have to be properly resolved at some stage in the future and preferably sooner, rather than later.

Added to the preceding was a second very poorly constructed paper by Cattaneo published in 2022 in an online publication called "*Biodiversity Journal*".

As for the first paper, I must state that if it was subject to any form of peer review it was either highly defective, or outright shambolic, as there is no way known that the latter paper should have ever been published in the form it was.

Again it is evident that he rushed it into print to scoop what he knew was an imminent paper from myself.

The basis of the newer paper was to erect a new subgenus for vipers within the Genus *Montivipera*.

Daboia xanthina Gray, 1849 is the type species of the genus *Montivipera* Nilson *et al*. 1999.

Cattaneo (2022) registered his paper with "Zoobank" as well as the subgenus *Planivipera* Cattaneo (2022) in a separate but associated

listing.
The Zoobank entry for the subgenus as of 1 Jan 2022 at:
https://zoobank.org/NomenclaturalActs/dcad3db3-0345-4287-a486-90dba4083bdd
was incomplete as it did not list a type species or page reference for the nomenclatural act.
That is not a serious misdemeanour in itself, but is sloppy nonetheless and should have been added as soon as the online paper was published.
It is however indicative of a rush to publish a new name and without taking all proper factors into consideration.
In spite of the preceding omission, the paper itself at page 791 lists "*Montivipera xanthina*" as the type species for his subgenus *Planivipera*, so that could of course be added to the Zoobank entry at any stage.
Significantly this means that in an act of egregious taxonomic vandalism he has created an objective junior synonym of "*Montivipera*" (same type species) and cluttered herpetology with yet another unwanted and unnecessary junior synonym.
Because *Planivipera* is an objective junior synonym, it cannot be properly used in herpetology, no matter what taxonomy or taxonomic freedom is used.
Significantly, Cattaneo (2022) did not cite or refer to the very relevant work of Hoser (2016) that dealt in detail with this very group of vipers, while simultaneously liberally citing works of Wuster *et al*., that referred to the Hoser works repeatedly, meaning he could not have been unaware of the earlier Hoser work of 2016 or the other relevant papers of Hoser with respect to the European and Middle-eastern Viperidae.
Of course the one (as of 2016) obvious subgenus in the *Montivipera xanthina* complex that needed to be named, had been formally named by Hoser in 2016 (namely *Apexvipera* Hoser, 2016, with a type species of *Vipera raddei* Boettger, 1890).
There remain many unnamed species of reptile in the world, including it seems, some viper species and to that extent, it would be helpful for persons such as Augusto Cattaneo to assist in this task of naming taxa and before some of them become extinct.
Outside of the Viperidae, there are thousands of reptile species awaiting formal scientific descriptions, meaning there is no need for him or anyone else in the same cohort to be renaming species or genera already named by others in the proper ICZN way.
However Cattaneo's repeated acts of rushing to print to name taxa to scoop a so-called rival (as he did in 2021) in a paper that may not even be code complaint, or as in the most recent case in 2022, to engage in direct taxonomic vandalism by renaming a genus named properly about 23 years earlier by Nilson *et al*. (1999a) is counterproductive and hampers both science and any wildlife conservation that may flow on from that.
The time wasted dealing with the consequences of taxonomic vandalism would be better spent dealing with new science, rather than repairing damage from what is better described as fake science.

SUMMARY OF SPECIES AND SUBSPECIES RECOGNIZED HEREIN

These are as follows:

1/ *Vipera ammodytes* (Linnaeus, 1758) (now taken as being within *Longumnaribussuis gen. nov.*) as the nominate form of the species is self-evidently recognized as valid.
Schwarz (1936) restricted the type locality of the holotype to Zadar, Croatia.
Assessment of available synonym names was based on the information published in *McDiarmid et al*. (1999) and Krecsák (2007), including citations therein.
Type *Vipera ammodytes* conforms with the north-west clade of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
Based on type localities of the various forms previously named within the *V. ammodytes* complex and the distribution of the clade as mapped by Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020), the following putative forms are herein treated as synonyms of this taxon.
V. illyrica Laurenti, 1768 from Italy.
V. fusca (Laurenti, 1768) from Italy.
V. pallidocaerulscens (Laurenti, 1768) from Italy.
V. velebitensis (Reuss, 1935) from the Velebit Mountains, Croatia.
V. litoralis (Reuss, 1935) from near Zadar, Croatia.
V. ruffoi (Bruno, 1968) from Italy.
V. gregorwallneri (Sochurek, 1974) from Austria.
2/ *V. connectens* (Bolkay, 1919) (now taken as being within *Longumnaribussuis gen. nov.*) with a type locality in Albania, is recognized herein as a valid species.
Bruno (1989) wrote:
"*Populations of North and Central Albania, north of the Shkumbin Valley, belong to the* ssp. ammodytes *(Linnaeus, 1758), whereas populations south of the Shkumbin Valley belong to* ssp. meridionalis *Boulenger, 1903. In the Plain of Mallakaster intermediate forms (*var. connectens *Bolkay, 1919) are present*."
In terms of *V. connectens*, this is the position taken herein.
The specimens in the north of Albania and including those from Montenegro, are herein treated as a new and separate species as per the phylogenies of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
The specimens south of Vlore, Albania and most of south-west Greece are also herein treated as a new and separate species as per the phylogenies of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
3/ *V. meridionalis* (Boulenger, 1903) (now taken as being within *Longumnaribussuis gen. nov.*) is recognized as a valid species-level taxon. However within putative *V. meridionalis* as currently understood by most herpetologists are several obvious species and subspecies, including as flagged by Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
Mertens and Muller (1940) proposed restricting the type locality to Athens, Greece and to effect this in order to stabilize the taxonomy and nomenclature of the species complex, a lectotype from the series of syntypes is designated now in this paper. That is specimen BMNH 1898.3.30.27 collected from Athens.
This is done in accordance with Article 74 of the *International Code of Zoological Nomenclature* (Ride *et al*. 1999).
This lectotype is now the unique bearer of the name of the nominal species-group taxon and the standard for its application (Articles 74.1 all parts, 74.3 all parts).
V. meridionalis as defined herein, conforms with the so-called southern clade of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
4/ *V. steindachneri* (Werner, 1897) (now taken as being within *Longumnaribussuis gen. nov.*) from west Romania is recognized as a valid species and conforms with the north-east clade of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
The putative taxon *V. melanura* (Reuss, 1937) from Serbia is herein regarded as a junior synonym of *V. steindachneri.*
5/ *V. montandoni* (Boulenger, 1904) (now taken as being within *Longumnaribussuis gen. nov.*) from eastern Romania is a valid species and conforms with the eastern clade as identified by Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).
The putative taxon *V. balcanica* Buresch and Zonkov, 1934 from south-east Bulgaria is regarded as a junior synonym of *V. montandoni.*
6/ *V. transcaucasiana* (Boulenger, 1913) (now taken as being within *Longumnaribussuis gen. nov.*) with a type locality of Borzom, Georgia is a valid species. It is apparently confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time.
The putative taxon, *V. transversovirgata* (Zarevsky, 1915) from the same type location as *V. transcaucasiana* is self-evidently a junior synonym of the earlier named taxon, that name therefore not being available for the East Turkey population.
The above comprise the six previously named species within the complex (excluding the more recently named *L. buchholzi* (Cattaneo, 2021), treated in the section immediately below as if a

newly named taxon.

The hitherto previously unnamed taxa that are formally named for the first time in this paper (including *L. buchholzi*) are as follows:

A/ *Longumnaribussuis montenegroensis sp. nov.* from Montenegro, shown as divergent by more than 5 MYA from all other clades by the studies of Ursenbacher *et al*. (2008), Roussos (2015) and Freitas *et al.* (2020).

B/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece was shown to have a divergence of more than 8 MYA from nearest relatives in the study of Roussos (2015).

C/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

D/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015) being *L. maxhoseri sp. nov*..

E/ *L. shireenhoserae sp. nov.* from west Turkey, was found to have a divergence of over 4 MYA from nearest relatives in the study of Roussos (2015).

F/ *L. buchholzi* (Cattaneo, 2021) from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), was found to have a divergence of over 8 MYA from nearest previously named relatives in the study of Roussos (2015).

In terms of the subspecies named herein, *L. buchholzi buchholzi* (Cattaneo, 2021) (type locality of Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA (named herein as subspecies) by Roussos (2015).

In terms of the relevant recognized taxa, Roussos (2015) said: "*The distances between the clades are well within the range of acceptable genetic distances to distinguish between species (1.01-19.1% [median 6.4%]) and subspecies level (median ~ 1.0%) in phylogenetic works involving herpetofauna (Torstrom* et al*. 2014) and even between new species in viperid studies (*Atheris matildae - Atheris ceratofora*, Menegon* et al. *2014*)."

Common sense dictates the recognition of the relevant listed taxa, including those formally described for the first time ever in this paper as subspecies as listed below.

G/ *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

I have hesitated to make this taxon a full species based on a belief Roussos (2015) may have over-estimated the divergence of the relevant taxa and also the geographical proximity of the island of Evia to the adjacent mainland allowing for potential gene flow in the recent past.

***H/ L. epirusensis lefkadaensis subsp. nov*.** from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA

I/ *L. buchholzi mykonosensis subsp. nov.* from the north Cyclades islands of Mykonos, Rinia and Tinos islands was shown by Roussos (2015) to have diverged from *L. buchholzi androsensis subsp. nov.* some 3.58 MYA.

J/ *L. buchholzi androsensis subsp. nov.* from the island of Andros, north Cyclades was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades) 2.3 MYA, and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) some 3.58 MYA.

K/ *L. buchholzi sirosensis* from Siros Island, north Cyclades, diverged some 2.3 MYA from the nearest related specimens (*L. buchholzi androsensis subsp. nov.*).

L/ *L. buchholzi naxosensis subsp. nov.* from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi buchholzi subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

M/ *L. buchholzi sikinosensis subsp. nov.* from Sikinos Island, South Cyclades is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

N/ *L. buchholzi koufonissiensis subsp. nov.* from Koufonissi island, South Cyclades was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

NOTES ON THE FORMAL DESCRIPTIONS THAT FOLLOW

In terms of the descriptions that follow, the following should be noted:

There is no conflict of interest in terms of this paper or the conclusions arrived at herein.

Several people including anonymous peer reviewers who revised the manuscript prior to publication are also thanked as are relevant staff at museums who made specimens and records available in line with international obligations.

In terms of the following formal descriptions, spellings should not be altered in any way for any purpose unless expressly and exclusively called for by the rules governing Zoological Nomenclature as administered by the International Commission on Zoological Nomenclature (ICZN) as published in the *International Code of Zoological Nomenclature* (Ride *et al*. 1999) ("The Code") as amended online since (ICZN 2012).

This includes if gender assignment of suffixes seems incorrect, Latinisation is wrong, apparent spelling mistakes and so on (see Article 32.5.1 of the Code).

In the unlikely event two or more newly named taxa are deemed to be the same by a first reviser, then the name to be used and retained is that which first appears in this paper by way of page priority and as listed in the abstract keywords.

Some material in descriptions for taxa may be repeated for other taxa in this paper and this is necessary to ensure each fully complies with the provisions of the *International Code of Zoological Nomenclature* (fourth edition) (Ride *et al.* 1999) as amended online since (ICZN 2012).

Material downloaded from the internet and cited anywhere in this paper was downloaded and checked most recently as of 10 August 2022 (including if also viewed prior), unless otherwise stated in the relevant text and was accurate in terms of the content cited herein as of that date.

Any online citations within this paper, including copied emails and the like, are not necessarily cited in the references part of this paper and have the same most recent viewing date as just given unless stated otherwise.

Unless otherwise stated explicitly, colour and other descriptions apply to living and **fully mature adult male specimens** of generally good health, as seen by day, and not under any form of stress by means such as excessive cool, heat, dehydration, excessive ageing, abnormal skin or reaction to chemical or other input.

The gender is important as there is sexual dimorphism in these species, with females commonly brownish in colour, versus greyish males from the same areas, or variants of this theme across the range for the genus, although this variation is self-evidently not consistent.

SVL or SV means snout-vent length, TL means tail length.

While numerous texts and references were consulted prior to publication of this paper, the criteria used to separate the relevant genera, subgenera, species or subspecies has already been spelt out and/or is done so within each formal description and does not rely on material within publications not explicitly cited herein.

FORMAL DESIGNATION OF A LECTOTYPE IN ACCORDANCE WITH THE *INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE*

The available name for the snake originally named as *Vipera ammodytes* Var. *meridionalis* Boulenger, 1903 was based on a syntype series from more than one location and therefore potentially including more than one species or subspecies.

In order to maintain stability of names in accordance with the

International Code of Zoological Nomenclature (Ride *et al*. 1999), I herein designate a Lectotype for the species or subspecies originally named as *Vipera ammodytes* Var. *meridionalis* Boulenger, 1903 in accordance with Article 74 of the *International Code of Zoological Nomenclature* (Ride *et al*. 1999) for the syntype animal, currently held at the Museum of Natural History, London, UK, specimen number 1898.3.30.27 being a specimen collected from Athens, Greece.

This lectotype is now the unique bearer of the name of the nominal species-group taxon and the standard for its application (Articles 74.1 all parts, 74.3 all parts).

LONGUMNARIBUSSUIS GEN. NOV.

LSIDurn:lsid:zoobank.org:act:66DA4E8B-F2D4-4013-89F5-5C18A2B5F396

Type species: *Longumnaribussuis shireenhoserae sp. nov.* (this paper).

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Distribution: Northern Italy, through southern Austria across the Balkans, including Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Kosovo, Montenegro, North Macedonia, Romania, Serbia, and Slovenia, as well as Greece, including the Cyclades and Turkey, across the southern shore of the Black Sea to Georgia.

Etymology: The genus name *Longumnaribussuis gen. nov.* comes from a merging of the Latin words, "*longum naribus suis*" which means, long nose or snout, in reflection of the prominent horn-like appendage on the snout of adult specimens.

Content: *Longumnaribussuis shireenhoserae* (type species); *L. ammodytes* (Linnaeus, 1758); *L. buchholzi* (Cattaneo, 2021); *L. connectens* (Bolkay, 1919); *L. epirusensis sp. nov.*; *L. mariolisi sp. nov.*; *L. maxhoseri sp. nov.*; *L. meridionalis* (Boulenger, 1903); *V. montandoni* (Boulenger, 1904); *L. montenegroensis sp. nov.*; *L. steindachneri* (Werner, 1897); *V. transcaucasiana* (Boulenger, 1913).

LONGUMNARIBUSSUIS MONTENEGROENSIS SP. NOV.

LSIDurn:lsid:zoobank.org:act:FEB7A7EF-5DB1-43B1-B0AD-23A8CCAAD19F

Holotype: A preserved specimen at the Naturalis Biodiversity Center, Leiden, The Netherlands, specimen number RMNH. RENA.10578 collected from Biogradsko jezero, Montenegro, Latitude 42.8962 N., Longitude 19.6018 E.

This facility allows access to its holdings.

Paratypes: 1/ A preserved specimen at the Naturalis Biodiversity Center, Leiden, The Netherlands, specimen number RMNH. RENA.38709 collected from Gradina, Dal van de Tara, Montenegro.

2/ A preserved specimen at the Natural History Museum, London, UK, specimen number 1898.10.10.26 collected from Montenegro.

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

L. ammodytes with a type locality of Zadar, Croatia, is the taxon found from Dubrovnik, Croatia in the south, along the coast to include the regions north-west of there, including Croatia, Slovenia, Austria and northern Italy.

It is separated from *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* by the following combination of characters: a light orange iris, usually, but not always a faded dorsal colouration and pattern, and if bold, then there is significant dark peppering on the lighter parts of the dorsum; few if any markings on the upper labials.

L. steindachneri (Werner, 1897) with a type locality of Banat, west Romania is the taxon from west Romania and nearby Croatia.

It is separated from *L. ammodytes*, *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* by the following suite of characters: Dark orange iris; bold and contrasting dark and light markings on the dorsum, with the mid dorsal dark markings in the form of an s-link pattern along the anterior and mid body, being of fairly even thickness along this part of the length of the body. The thickness does not occillate from extremely wide to extremely narrow as seen in the other three species. Few if any markings on the upper labials.

L. montenegroensis sp. nov. with a type locality of Biogradsko jezero, in eastern Montenegro is found in most parts of Montenegro and nearby parts of northern Albania, south to about the Shkumbin Valley.

It is separated from *L. ammodytes*, *L. connectens* (Bolkay, 1919) and *L. steindachneri* (Werner, 1897) by the following suite of characters: Iris, light orange-yellow; usually, but not always of the red phase (as opposed to grey), but regardless of phase the mid-dorsal line is prominently black etched on the outer (lateral) edges and lighter orange (or grey) in the inner areas (versus barely detectable in *L. steindachneri* and *L. ammodytes*). Lighter lateral parts of dorsum often, but not always have dark interstitial skin that is prominent. Upper labials are either white or whitish, often combined with a prominent backward running white stripe, and any darker parts are either absent or in the form of small triangles on the upper lip, not reaching the eye. Mid-dorsal markings on the anterior and mid body are of the form of diamonds or triangles that are narrowly joined at the apexes, as one runs down the mid-dorsal line.

L. connectens (Bolkay, 1919), is apparently restricted to the plain of Mallakaster in Albania, with *L. montenegroensis sp. nov.* occurring north of there and *L. epirusensis sp. nov.* south of there.

L. connectens is invariably of a greyish or brownish colouration dorsally, and readily separated from *L. ammodytes*, *L. steindachneri* and *L. montenegroensis sp. nov.* by the fact that the horn-like appendage on the snout points forward at a slight angle, rather than more obviously as seen in the other three species.

In *L. epirusensis sp. nov.* and all other members of the genus *Longumnaribussuis gen. nov.* the horn like appendage points up (rather than forward), although in some specimens the upper part is bent forward.

L. connectens is further separated from *L. ammodytes*, *L. steindachneri* and *L. montenegroensis sp. nov.* by having a beige iris; an obviously white upper labial region, with one or more dark brown bars extending from lip to eye; mid-dorsal dark markings in the form of diamonds joined top and bottom to one another along the spine, being brown centred and with well defined and strongly contrasting narrow black edges on the outer edges and bordering the light background colour of the other parts of the dorsum (versus not strongly contrasting in *L. montenegroensis sp. nov.*).

L. montenegroensis sp. nov. in life is depicted online at:
http://en.balcanica.info/2-680
and
http://en.balcanica.info/2-678
and
http://en.balcanica.info/2-12040
and
https://m.facebook.com/336124553250145/photos/vipera-ammodytes-ammodytesmontenegro/400037636858836/

L. ammodytes in life is depicted in Phelps (2010) on pages 445 and 446 at top as well as online at:
online at:
https://www.inaturalist.org/observations/72260240
and
https://www.inaturalist.org/observations/122775357
and
https://www.inaturalist.org/observations/26665113

L. steindachneri in life is depicted online at:
https://www.inaturalist.org/observations/130471482
and
https://www.inaturalist.org/observations/130474822
and
https://www.inaturalist.org/observations/264705

L. connectons in life is depicted online at:
https://www.inaturalist.org/observations/103439277
and
https://www.inaturalist.org/observations/93282084

L. epirusensis sp. nov. in life is depicted online at:
https://www.inaturalist.org/observations/116563984
and
https://www.inaturalist.org/observations/79169505
and
https://www.inaturalist.org/observations/5073276

Distribution: *L. montenegroensis sp. nov.* with a type locality of Biogradsko jezero, in eastern Montenegro is found in most parts of Montenegro and nearby parts of northern Albania, south to about the Shkumbin Valley.

Etymology: The new species *L. montenegroensis sp. nov.* is named in reflection of both the type locality and the centre of distribution for the species.

LONGUMNARIBUSSUIS EPIRUSENSIS SP. NOV.
LSIDurn:lsid:zoobank.org:act:A5081EE2-3DF6-460F-996F-134B6A1A80E1

Holotype: A preserved specimen at the Museum of Natural History, London, UK, specimen number NHMUK ZOO BMNH 1987.1396 collected from Mount Pantokratar, Corfu, Greece, Latitude 39.7469 N., Longitude 19.8711 E.

This facility allows access to its holdings.

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It

also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge. Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

Venter is invariably darker or with darker markings of some form.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* (Cattaneo, 2021) in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.
Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.
Iris is grey.
L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.
The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.
By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.
The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..
L. meridionalis in life is depicted online at:
https://www.inaturalist.org/observations/83625956
and
https://www.inaturalist.org/observations/128073549
and
https://www.inaturalist.org/observations/108664042
and
https://www.flickr.com/photos/thorhakonsen/33185905068/
and
https://www.flickr.com/photos/thorhakonsen/47083251931/
and
https://www.flickr.com/photos/thorhakonsen/33954187174/
L. meridionalis eviaensis sp. nov. from Karistos, Evia Island, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/87543738
L. montandoni is depicted online at:
https://www.researchgate.net/figure/A-female-Vipera-ammodytes-montandoni-from-a-karst-region-in-central-north-Bulgaria_fig3_313012719
and
https://www.flickr.com/photos/55114263@N00/34209413433
and
https://www.flickr.com/photos/55114263@N00/34209413583/
L. melanura in life is depicted online at:
https://www.inaturalist.org/observations/130471482
and
https://www.inaturalist.org/observations/130474822
and
https://www.inaturalist.org/observations/264705
L. epirusensis sp. nov. from Corfu, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/116563984
and
https://www.inaturalist.org/observations/79169505
and
https://www.inaturalist.org/observations/5073276
L. epirusensis lefkadaensis subsp. nov. from Lefkada Island, Greece, in life is depicted online at:
http://www.focusnatura.at/serpentes-schlangen-snakes/
and
https://www.researchgate.net/figure/Herpetofauna-observed-by-the-authors-on-Lefkada-Erpetofauna-osservata-dagli-autori-a_fig2_346108093
and
http://www.viperas.de/Lefkada.html
L. maxhoseri sp. nov. in life is depicted online at:
https://www.flickr.com/photos/162809684@N05/51875706511/
and
https://www.flickr.com/photos/162160385@N03/49086752823/
L. mariolisi sp. nov. in life from Kefalonia, Greece is depicted online at:
http://en.balcanica.info/2-8949
and
http://en.balcanica.info/2-8948
and
https://www.flickr.com/photos/adrien2008/32231326658
and
https://www.flickr.com/photos/adrien2008/45190887515/
L. buchholzi buchholzi of the nominate subspecies from Antiparos Island, Greece is depicted in life online at:
https://www.instagram.com/p/vxnZtuOT3l/
L. buchholzi sirosensis from Siros island, Greece is depicted in life online at:
https://www.alamy.com/stock-photo-eastern-sand-viper-vipera-ammodytes-meridionalis-near-delphini-beach-75367988.html
and
https://www.alamy.com/stock-photo-eastern-sand-viper-vipera-ammodytes-meridionalis-near-delphini-beach-75368006.html
L. buchholzi mykonosensis subsp. nov. from Tinos Island, Greece is depicted in life online at:
https://stock.adobe.com/au/images/nose-horned-viper-tinos-greece-europaische-hornotter-vipera-ammodytes-meridionalis-tinos-griechenland/330551196
and
https://stock.adobe.com/images/nose-horned-viper-tinos-greece-europaische-hornotter-vipera-ammodytes-meridionalis-tinos-griechenland/330553324
L. buchholzi androsensis subsp. nov. from Andros Island, Greece is depicted in life online at:
https://inaturalist.ala.org.au/observations/68955932
L. buchholzi naxosensis subsp. nov. from Ios Island, Greece is depicted in life online at:
https://www.alamy.com/male-nose-horned-viper-vipera-ammodytes-on-the-greek-island-of-ios-cyclades-islands-greece-image331029837.html?imageid=FCD31E55-BA20-4D0A-854C-8B57EFC22188&p=577683&pn=1&searchId=c2929a9e0e14d21c86d36ef200ae48de&searchtype=0
and
https://www.alamy.com/male-nose-horned-viper-vipera-ammodytes-on-the-greek-island-of-ios-cyclades-islands-greece-image331029873.html?imageid=F079C5C6-D3FF-4D4C-A415-2012962BDDCF&p=577683&pn=1&searchId=c2929a9e0e14d21c86d36ef200ae48de&searchtype=0
L. buchholzi sikinosensis subsp. nov. from Sikinos Island, Greece is depicted in life online at:
https://mwilsonherps.com/greece-trips/cyclades-2014/
and
https://mwilsonherps.files.wordpress.com/2014/07/img_5045-copy.jpg
L. buchholzi koufonissiensis subsp. nov. from Ano Koufonissi Island, Greece is depicted in life online at:
https://mwilsonherps.com/greece-trips/koufonisia-small-cyclades-new/
L. transcaucasiana in life is depicted online at:
https://www.inaturalist.org/observations/117763482
and
https://www.inaturalist.org/observations/130076887
and
https://www.inaturalist.org/observations/15631414
L. shireenhoserae sp. nov. in life is depicted in Akkaya (2012) on page 184 at top and online at:
https://www.inaturalist.org/observations/60605411
Distribution: *L. epirusensis sp. nov*. has a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, Greece, extending north to far southern Albania, south of the Shhumbin Valley and the Plain of Mallakaster.
Etymology: *L. epirusensis sp. nov*. is named in reflection of where it occurs.

LONGUMNARIBUSSUIS EPIRUSENSIS LEFKADAENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:D46DB0CC-3332-4D08-ABF1-064FB8255F46

Holotype: A road-killed adult specimen on Lefkada Island, depicted in an image by Sindaco and Rossi (2020) on page 62 in Fig. 3., Photo D. The publication is available online as a pdf at: https://www.researchgate.net/publication/346108093_Annotated_checklist_of_the_herpetofauna_Amphibia_Reptilia_of_Lefkada_Island_Ionian_Islands_Greece

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.

Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is

beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have

diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

L. meridionalis in life is depicted online at:
https://www.inaturalist.org/observations/83625956
and
https://www.inaturalist.org/observations/128073549
and
https://www.inaturalist.org/observations/108664042
and
https://www.flickr.com/photos/thorhakonsen/33185905068/
and
https://www.flickr.com/photos/thorhakonsen/47083251931/
and
https://www.flickr.com/photos/thorhakonsen/33954187174/

L. meridionalis eviaensis sp. nov. from Karistos, Evia Island, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/87543738

L. montandoni is depicted online at:
https://www.researchgate.net/figure/A-female-Vipera-ammodytes-montandoni-from-a-karst-region-in-central-north-Bulgaria_fig3_313012719
and
https://www.flickr.com/photos/55114263@N00/34209413433
and
https://www.flickr.com/photos/55114263@N00/34209413583/

L. melanura in life is depicted online at:
https://www.inaturalist.org/observations/130471482
and
https://www.inaturalist.org/observations/130474822
and
https://www.inaturalist.org/observations/264705

L. epirusensis sp. nov. from Corfu, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/116563984
and
https://www.inaturalist.org/observations/79169505
and
https://www.inaturalist.org/observations/5073276

L. epirusensis lefkadaensis subsp. nov. from Lefkada Island, Greece, in life is depicted online at:
http://www.focusnatura.at/serpentes-schlangen-snakes/

and
https://www.researchgate.net/figure/Herpetofauna-observed-by-the-authors-on-Lefkada-Erpetofauna-osservata-dagli-autori-a_fig2_346108093
and
http://www.viperas.de/Lefkada.html
For diagnostic information separating each of the other seven species and relevant subspecies from one another, please refer to the preceding description for *L. epirusensis sp. nov*., referred to herein as part of this formal description.
Distribution: *L. epirusensis lefkadaensis subsp. nov*. is a range-restricted endemic confined to Lefkada and Ithaki Islands, south-west Greece
Etymology: *L. epirusensis lefkadaensis subsp. nov*. is named in reflection of both type locality and the largest island on which it occurs.
LONGUMNARIBUSSUIS MERIDIONALIS EVIAENSIS SUBSP. NOV.
LSIDurn:lsid:zoobank.org:act:247A2965-54C7-470D-99B4-30E5D1E6EDDA
Holotype: A live adult specimen depicted online at:
https://www.inaturalist.org/observations/87543738
photographed on 18 July 2021 at Karistos, Evia (Evvoia) Island, Greece.
Paratype: A dead specimen from the north of Evia (Evvoia) Island, Greece depicted online at:
https://www.inaturalist.org/observations/29010509
Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.
Species in this genus are separated from all other Viperidae by the following unique combination of characters:
Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.
Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.
Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.
In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.
Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:
1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.
2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.
3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergent of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.
4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..
5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).
6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.
7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.
8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).
L. meridionalis are separated from the other seven species and relevant subspecies by the following unique combination of characters:
L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.
The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.
The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.
L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.
The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.
The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.
This gives the subspecies are very different appearance than that of the nominate form.
There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.
L. meridionalis in life is depicted online at:
https://www.inaturalist.org/observations/83625956
and

https://www.inaturalist.org/observations/128073549
and
https://www.inaturalist.org/observations/108664042
and
https://www.flickr.com/photos/thorhakonsen/33185905068/
and
https://www.flickr.com/photos/thorhakonsen/47083251931/
and
https://www.flickr.com/photos/thorhakonsen/33954187174/
L. meridionalis eviaensis sp. nov. from Karistos, Evia Island, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/87543738
For diagnostic information separating each of the other seven species and relevant subspecies from one another, please refer to the preceding description for *L. epirusensis sp. nov*., referred to herein as part of this formal description.

Distribution: *L. meridionalis eviaensis sp. nov.* is confined to Evia (Evvoia) Island, Greece.

Etymology: *L. meridionalis eviaensis sp. nov.* is named in reflection of the type locality and where it occurs, being Evia (Evvoia) Island, Greece.

LONGUMNARIBUSSUIS MAXHOSERI SP. NOV.

LSIDurn:lsid:zoobank.org:act:D626BB5F-35D4-4639-8E3F-99D426892933

Holotype: A preserved specimen at the Vertebrate Zoology Division, Herpetology, Yale Peabody Museum, New Haven, Connecticut, USA, specimen number YPM HERR 005756 collected from the Korinthia Province, Peloponnisos Region, Greece.
This facility allows access to its holdings.

Paratypes: 1/ A preserved specimen in the Natural History Museum, London, UK, specimen number 1972.1130 collected from 10 km south-west of Kiaton, North Peloponnes, Greece, and 2/ A preserved specimen in the Natural History Museum, London, UK, specimen number 1892.9.19.23 collected from near Tarsos, North Morea, Greece.

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.
Species in this genus are separated from all other Viperidae by the following unique combination of characters:
Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.
Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.
Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.
In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.
Based on the preceding, the remaining species within *Longumnaribussuis gen. nov.* are as follows:
1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.
2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.
3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.
4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..
5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).
6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.
7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.
8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).
L. maxhoseri sp. nov. is separated from the other seven species, including subspecies of some of these, by the following unique suite of characters:
L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.
L. maxhoseri sp. nov. in life is depicted online at:
https://www.flickr.com/photos/162809684@N05/51875706511/
and
https://www.flickr.com/photos/162160385@N03/49086752823/
For diagnostic information separating each of the other seven species and relevant subspecies from one another, please refer to the preceding description for *L. epirusensis sp. nov*., referred to herein as part of this formal description.

Distribution: *L. maxhoseri sp. nov*. is confined to the Peloponnese Region of south-west Greece.

Etymology: *L. maxhoseri sp. nov*. is named in honour of my cousin, Max Hoser of Campbelltown, south-western Sydney, New South Wales, Australia in recognition of his contributions to herpetology in the 1970's and 1980's.

LONGUMNARIBUSSUIS MARIOLISI SP. NOV.

LSIDurn:lsid:zoobank.org:act:701544F4-86EB-4D75-A04C-568E27C9D1A0

Holotype: A live specimen depicted in the image posted online at:
http://en.balcanica.info/2-8949
photographed by Marek Jedlička on 4 April 2011 collected 720 m ASL at Omala, Kefalonia, Greece.

Diagnosis: The complex of species within the genus

Longumnaribussuis gen. nov. has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

L. maxhoseri sp. nov. and the morphologically similar *L. mariolisi sp. nov*. are separated from the other six species by the following suites of characters:

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri* sp. *nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. maxhoseri sp. nov. in life is depicted online at:
https://www.flickr.com/photos/162809684@N05/51875706511/
and
https://www.flickr.com/photos/162160385@N03/49086752823/

L. mariolisi sp. nov. in life from Kefalonia, Greece is depicted online at:
http://en.balcanica.info/2-8949
and
http://en.balcanica.info/2-8948
and
https://www.flickr.com/photos/adrien2008/32231326658
and
https://www.flickr.com/photos/adrien2008/45190887515/

For diagnostic information separating each of the other six species and relevant subspecies from one another, please refer to the preceding description for *L. epirusensis sp. nov*., referred to herein as part of this formal description.

Distribution: *L. mariolisi sp. nov*. is confined to Kefalonia Island, south-west Greece, and apparently separated from congeners by a historical deep sea barrier.

Etymology: *L. mariolisi sp. nov*. is named in honour of George Mariolis, formerly of Burwood, Victoria, Australia, now of the Sunshine Coast, Queensland, Australia, former owner of Definition Fitness Centre in East Doncaster, husband of internationally recognized fitness expert, Karla Gambell both of whom for decades has been among the most highly regarded personal trainers in Australia in recognition of their amazing work in transforming lives for the better of clients and others he mixes with.

In their younger days, both were elite grade body builders and part of the "who's who" in that fraternity (globally).

***LONGUMNARIBUSSUIS BUCHHOLZI* (CATTANEO, 2021)**
Tentatively recognized herein as a valid nomen (see explanation earlier in this paper).

Type locality: Antiparos Island.

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is

sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.

Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side

blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-

grey.
A thin brownish-black line runs from the bottom of the eye to the back of the head.
The side blotches are in the form of semi-distinct brown triangles.
Iris is beige.
L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).
L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.
L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.
L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).
Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.
The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.
L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).
Characters unique to the nominate subspecies *L. buchholzi buchholzi* in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.
Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.
Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.
The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.
The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.
In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.
Each blotch has become in effect a narrow rectangle across the back (length running side to side).
The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.
In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.
The head is of the lighter background colour with obvious heavy peppering or spotting.
Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.
Iris is grey.
L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.
The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.
By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.
The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..
L. meridionalis in life is depicted online at:
https://www.inaturalist.org/observations/83625956
and
https://www.inaturalist.org/observations/128073549
and
https://www.inaturalist.org/observations/108664042
and
https://www.flickr.com/photos/thorhakonsen/33185905068/
and
https://www.flickr.com/photos/thorhakonsen/47083251931/
and
https://www.flickr.com/photos/thorhakonsen/33954187174/
L. meridionalis eviaensis sp. nov. from Karistos, Evia Island, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/87543738
L. montandoni is depicted online at:
https://www.researchgate.net/figure/A-female-Vipera-ammodytes-montandoni-from-a-karst-region-in-central-north-Bulgaria_fig3_313012719
and
https://www.flickr.com/photos/55114263@N00/34209413433
and
https://www.flickr.com/photos/55114263@N00/34209413583/
L. melanura in life is depicted online at:
https://www.inaturalist.org/observations/130471482
and
https://www.inaturalist.org/observations/130474822
and
https://www.inaturalist.org/observations/264705
L. epirusensis sp. nov. from Corfu, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/116563984
and
https://www.inaturalist.org/observations/79169505
and
https://www.inaturalist.org/observations/5073276
L. epirusensis lefkadaensis subsp. nov. from Lefkada Island, Greece, in life is depicted online at:
http://www.focusnatura.at/serpentes-schlangen-snakes/
and
https://www.researchgate.net/figure/Herpetofauna-observed-by-the-authors-on-Lefkada-Erpetofauna-osservata-dagli-autori-a_fig2_346108093
and
http://www.viperas.de/Lefkada.html
L. maxhoseri sp. nov. in life is depicted online at:
https://www.flickr.com/photos/162809684@N05/51875706511/
and
https://www.flickr.com/photos/162160385@N03/49086752823/
L. mariolisi sp. nov. in life from Kefalonia, Greece is depicted online at:
http://en.balcanica.info/2-8949

and
http://en.balcanica.info/2-8948
and
https://www.flickr.com/photos/adrien2008/32231326658
and
https://www.flickr.com/photos/adrien2008/45190887515/
L. buchholzi buchholzi of the nominate subspecies from Antiparos Island, Greece is depicted in life online at:
https://www.instagram.com/p/vxnZtuOT3l/
L. buchholzi sirosensis from Siros island, Greece is depicted in life online at:
https://www.alamy.com/stock-photo-eastern-sand-viper-vipera-ammodytes-meridionalis-near-delphini-beach-75367988.html
and
https://www.alamy.com/stock-photo-eastern-sand-viper-vipera-ammodytes-meridionalis-near-delphini-beach-75368006.html
L. buchholzi mykonosensis subsp. nov. from Tinos Island, Greece is depicted in life online at:
https://stock.adobe.com/au/images/nose-horned-viper-tinos-greece-europaische-hornotter-vipera-ammodytes-meridionalis-tinos-griechenland/330551196
and
https://stock.adobe.com/images/nose-horned-viper-tinos-greece-europaische-hornotter-vipera-ammodytes-meridionalis-tinos-griechenland/330553324
L. buchholzi androsensis subsp. nov. from Andros Island, Greece is depicted in life online at:
https://inaturalist.ala.org.au/observations/68955932
L. buchholzi naxosensis subsp. nov. from Ios Island, Greece is depicted in life online at:
https://www.alamy.com/male-nose-horned-viper-vipera-ammodytes-on-the-greek-island-of-ios-cyclades-islands-greece-image331029837.html?imageid=FCD31E55-BA20-4D0A-854C-8B57EFC22188&p=577683&pn=1&searchId=c2929a9e0e14d21c86d36ef200ae48de&searchtype=0
and
https://www.alamy.com/male-nose-horned-viper-vipera-ammodytes-on-the-greek-island-of-ios-cyclades-islands-greece-image331029873.html?imageid=F079C5C6-D3FF-4D4C-A415-2012962BDDCF&p=577683&pn=1&searchId=c2929a9e0e14d21c86d36ef200ae48de&searchtype=0
L. buchholzi sikinosensis subsp. nov. from Sikinos Island, Greece is depicted in life online at:
https://mwilsonherps.com/greece-trips/cyclades-2014/
and
https://mwilsonherps.files.wordpress.com/2014/07/img_5045-copy.jpg
L. buchholzi koufonissiensis subsp. nov. from Ano Koufonissi Island, Greece is depicted in life online at:
https://mwilsonherps.com/greece-trips/koufonisia-small-cyclades-new/
L. transcaucasiana in life is depicted online at:
https://www.inaturalist.org/observations/117763482
and
https://www.inaturalist.org/observations/130076887
and
https://www.inaturalist.org/observations/15631414
L. shireenhoserae sp. nov. in life is depicted in Akkaya (2012) on page 184 at top and online at:
https://www.inaturalist.org/observations/60605411

Distribution: *L. buchholzi* occurs on the northern and southern Cyclades, Greece.

The nominate subspecies *L. buchholzi buchholzi* (Cattaneo, 2021) occurs on the small Islands of Antiparos, and Despotiko, southern Cyclades, Greece.

Etymology: Refer to Cattaneo (2021).

LONGUMNARIBUSSUIS BUCHHOLZI SIROSENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:6876FBAF-E0C4-4B08-B7E4-C0AB9695B05D

Holotype: A preserved specimen at the Vertebrate Zoology Division, Herpetology, Yale Peabody Museum, New Haven, Connecticut, USA, specimen number YPM HERR 005757 collected from Mount Pyrgos, Siros (AKA Syros) Island, Cyclades Group, Greece, at 396 m ASL, Latitude 37.5000 N., Longitude 24.9167 E. This facility allows access to its holdings.

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of

Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye

as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands

running across the dorsal surface, sometimes onto the flanks and sometimes not.
Each blotch has become in effect a narrow rectangle across the back (length running side to side).
The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.
In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.
The head is of the lighter background colour with obvious heavy peppering or spotting.
Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.
Iris is grey.
L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.
The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.
By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.
The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..
L. meridionalis in life is depicted online at:
https://www.inaturalist.org/observations/83625956
and
https://www.inaturalist.org/observations/128073549
and
https://www.inaturalist.org/observations/108664042
and
https://www.flickr.com/photos/thorhakonsen/33185905068/
and
https://www.flickr.com/photos/thorhakonsen/47083251931/
and
https://www.flickr.com/photos/thorhakonsen/33954187174/
L. meridionalis eviaensis sp. nov. from Karistos, Evia Island, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/87543738
L. montandoni is depicted online at:
https://www.researchgate.net/figure/A-female-Vipera-ammodytes-montandoni-from-a-karst-region-in-central-north-Bulgaria_fig3_313012719
and
https://www.flickr.com/photos/55114263@N00/34209413433
and
https://www.flickr.com/photos/55114263@N00/34209413583/
L. melanura in life is depicted online at:
https://www.inaturalist.org/observations/130471482
and
https://www.inaturalist.org/observations/130474822
and
https://www.inaturalist.org/observations/264705
L. epirusensis sp. nov. from Corfu, Greece, in life is depicted online at:
https://www.inaturalist.org/observations/116563984
and
https://www.inaturalist.org/observations/79169505
and
https://www.inaturalist.org/observations/5073276
L. epirusensis lefkadaensis subsp. nov. from Lefkada Island, Greece, in life is depicted online at:
http://www.focusnatura.at/serpentes-schlangen-snakes/
and
https://www.researchgate.net/figure/Herpetofauna-observed-by-the-authors-on-Lefkada-Erpetofauna-osservata-dagli-autori-a_fig2_346108093
and
http://www.viperas.de/Lefkada.html
L. maxhoseri sp. nov. in life is depicted online at:
https://www.flickr.com/photos/162809684@N05/51875706511/
and
https://www.flickr.com/photos/162160385@N03/49086752823/
L. mariolisi sp. nov. in life from Kefalonia, Greece is depicted online at:
http://en.balcanica.info/2-8949
and
http://en.balcanica.info/2-8948
and
https://www.flickr.com/photos/adrien2008/32231326658
and
https://www.flickr.com/photos/adrien2008/45190887515/
L. buchholzi buchholzi of the nominate subspecies from Antiparos Island, Greece is depicted in life online at:
https://www.instagram.com/p/vxnZtuOT3l/
L. buchholzi sirosensis from Siros island, Greece is depicted in life online at:
https://www.alamy.com/stock-photo-eastern-sand-viper-vipera-ammodytes-meridionalis-near-delphini-beach-75367988.html
and
https://www.alamy.com/stock-photo-eastern-sand-viper-vipera-ammodytes-meridionalis-near-delphini-beach-75368006.html
L. buchholzi mykonosensis subsp. nov. from Tinos Island, Greece is depicted in life online at:
https://stock.adobe.com/au/images/nose-horned-viper-tinos-greece-europaische-hornotter-vipera-ammodytes-meridionalis-tinos-griechenland/330551196
and
https://stock.adobe.com/images/nose-horned-viper-tinos-greece-europaische-hornotter-vipera-ammodytes-meridionalis-tinos-griechenland/330553324
L. buchholzi androsensis subsp. nov. from Andros Island, Greece is depicted in life online at:
https://inaturalist.ala.org.au/observations/68955932
L. buchholzi naxosensis subsp. nov. from Ios Island, Greece is depicted in life online at:
https://www.alamy.com/male-nose-horned-viper-vipera-ammodytes-on-the-greek-island-of-ios-cyclades-islands-greece-image331029837.html?imageid=FCD31E55-BA20-4D0A-854C-8B57EFC22188&p=577683&pn=1&searchId=c2929a9e0e14d21c86d36ef200ae48de&searchtype=0
and
https://www.alamy.com/male-nose-horned-viper-vipera-ammodytes-on-the-greek-island-of-ios-cyclades-islands-greece-image331029873.html?imageid=F079C5C6-D3FF-4D4C-A415-2012962BDDCF&p=577683&pn=1&searchId=c2929a9e0e14d21c86d36ef200ae48de&searchtype=0
L. buchholzi sikinosensis subsp. nov. from Sikinos Island, Greece is depicted in life online at:
https://mwilsonherps.com/greece-trips/cyclades-2014/
and
https://mwilsonherps.files.wordpress.com/2014/07/img_5045-copy.jpg
L. buchholzi koufonissiensis subsp. nov. from Ano Koufonissi Island, Greece is depicted in life online at:
https://mwilsonherps.com/greece-trips/koufonisia-small-cyclades-new/
L. transcaucasiana in life is depicted online at:
https://www.inaturalist.org/observations/117763482
and
https://www.inaturalist.org/observations/130076887
and
https://www.inaturalist.org/observations/15631414

L. shireenhoserae sp. nov. in life is depicted in Akkaya (2012) on page 184 at top and online at:
https://www.inaturalist.org/observations/60605411
Distribution: *L. buchholzi* is a species complex from the Cyclades islands, southern Greece. Various subspecies are found on particular islands and species groups as formally named in this paper.
L. buchholzi sirosensis subsp. nov. is confined to Siros (AKA Syros) in the northern Cyclades islands, southern Greece.
Etymology: *L. buchholzi sirosensis subsp. nov*. is named in reflection of the island it occurs on.

LONGUMNARIBUSSUIS BUCHHOLZI MYKONOSENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:EEFC178F-F0B0-47B4-9F2A-A484444996B0

Holotype: A preserved specimen at the Museum of Natural History, London, UK, specimen number BMNH 1988.52, collected from Mykonos Island, Cyclades, Greece.
This facility allows access to its holdings.
Paratypes: 1/ A preserved specimen at the Vertebrate Zoology Division, Herpetology, Yale Peabody Museum, New Haven, Connecticut, USA, specimen number YPM HERP 000428 collected from Delos, Cyclades, Greece, and 2/ Two preserved specimens at the Naturalis Biodiversity Center, Leiden, The Netherlands, specimen number specimen number ZMA.RENA.10706 collected from Delos, Cyclades, Greece.
Diagnosis: *L. buchholzi mykonosensis subsp. nov.* which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros (AKA Syros) Island, north Cyclades), some 2.3 MYA.
The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.
Species in this genus are separated from all other Viperidae by the following unique combination of characters:
Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.
Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.
Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.
In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.
Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:
1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.
2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.
3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.
4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov.*.
5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).
6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.
7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.
8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).
The preceding eight species are separated from one another by the following unique combinations of characters:
L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.
The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.
The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.
L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.
The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.
The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.
This gives the subspecies are very different appearance than that of the nominate form.
There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis* (type locality Siros (AKA Syros) Island, north Cyclades), (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold

black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* (Cattaneo, 2021) in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

For images of the relevant taxa refer to the preceding formal description of *L. buchholzi sirosensis subsp. nov.*.

Distribution: *L. buchholzi mykonosensis subsp. nov*. occurs on the islands of Mykonos, Tinos, Rinia, Delos, in the Cyclades, Greece.

Etymology: *L. buchholzi mykonosensis subsp. nov*. is named in reflection of the type locality for the subspecies.

LONGUMNARIBUSSUIS BUCHHOLZI ANDROSENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:7EA651AB-79C8-4530-AD2C-6866326E99A3

Holotype: A live specimen photographed by Erwin Sieben, of KwaZulu-Natal, South Africa on 12 April 2000 at Andros Island, Greece, depicted in the image posted online at: https://inaturalist.ala.org.au/observations/68955932

Diagnosis: The subspecies *L. buchholzi androsensis subsp. nov.* from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis*

subsp. nov. from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) some 3.58 MYA.

The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.

Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the

anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* (Cattaneo, 2021) in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

For images of the relevant taxa refer to the preceding formal description of *L. buchholzi sirosensis subsp. nov.*.

Distribution: *L. buchholzi androsensis subsp. nov*. is confined to Andros Island, Greece.

Etymology: *L. buchholzi androsensis subsp. nov*. is named in reflection of the type locality and where the taxon is found.

LONGUMNARIBUSSUIS BUCHHOLZI NAXOSENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:67F9276D-DAF9-4774-8C2F-34C7261BF7F6

Holotype: A preserved specimen at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, specimen number USNM Amphibians and Reptiles 162258 collected from Naxos, Cyclades, Greece.

This facility allows access to its holdings.

Paratypes: 1/ A preserved specimen at the Vertebrate Zoology Division, Herpetology, Yale Peabody Museum, New Haven, Connecticut, USA, specimen number YPM HERR 005770 collected from 5 km from Khora, on the north coast of Naxos Island, Cyclades, Greece, Latitude 37.1000 N., Longitude 25.4000 E., 2/ A preserved specimen at the Vertebrate Zoology Division, Herpetology, Yale Peabody Museum, New Haven, Connecticut, USA, specimen number YPM HERR 005759 collected from Mount Prophet Ilias, Paros Island, Greece., 3/ A preserved specimen at the Museum of Natural History, London, UK, specimen number NHMUK ZOO 1987.1397 collected from Paros Island, Cyclades, Greece.

Diagnosis: *L. buchholzi naxosensis subsp. nov.* from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades, Greece (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (being the three subspecies *L. buchholzi buchholzi subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies at least 2.57 MYA.

The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper

labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another

quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to

L. buchholzi naxosensis subsp. nov. but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

For images of the relevant taxa refer to the preceding formal description of *L. buchholzi sirosensis subsp. nov.*.

Distribution: *L. buchholzi naxosensis subsp. nov.* is found on the Islands of Naxos, Paros, Iraklia and Ios in the southern Cyclades, Greece.

Etymology: *L. buchholzi naxosensis subsp. nov.* is named in reflection of the type locality of the taxon.

LONGUMNARIBUSSUIS BUCHHOLZI SIKINOSENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:2780CB7D-7784-43F9-A991-95E7EB7D2400

Holotype: A live specimen photographed by Matt Wilson in mid 2014 at Sikinos Island, Cyclades, Greece, depicted in an image posted at:
https://mwilsonherps.files.wordpress.com/2014/07/img_5045-copy.jpg

Diagnosis: The subspecies *L. buchholzi sikinosensis subsp. nov.* from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.

Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest

named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not

anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021) defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-

defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

Distribution: *L. buchholzi sikinosensis subsp. nov.* is found on the Island of Sikinos in the southern Cyclades, Greece.

Etymology: *L. buchholzi sikinosensis subsp. nov.* is named in reflection of the type locality of the taxon.

LONGUMNARIBUSSUIS BUCHHOLZI KOUFONISSIENSIS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:B78999B5-277A-48A4-97EB-4F3AA025A70F

Holotype: A live adult male specimen of a snake photographed by Matt Wilson in October 2016 at Koufonisia (aka Koufonissi) Island, Cyclades, Greece, depicted in an image posted at:
https://i0.wp.com/mwilsonherps.com/wp-content/uploads/2016/10/img_9924-copy.jpg

Paratype: A live adult female specimen of a snake photographed by Matt Wilson in October 2016 at Koufonisia (aka Koufonissi) Island, Cyclades, Greece, depicted in an image posted at:
https://i0.wp.com/mwilsonherps.com/wp-content/uploads/2016/10/img_0005-copy.jpg

Diagnosis: The subspecies *L. buchholzi koufonissiensis subsp. nov.* from Koufonissi island, Cyclades, Greece was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015). The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye. Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It

also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge. Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades) some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head.

The side blotches are in the form of semi-distinct brown triangles.

Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021), defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species.

In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

For images of the relevant taxa refer to the preceding formal description of *L. buchholzi sirosensis subsp. nov.*.

Distribution: *L. buchholzi koufonissiensis subsp. nov.* is found on small the Island of Koufonissi island (aka Koufonissi), southern Cyclades, Greece.

Etymology: *L. buchholzi koufonissiensis subsp. nov.* is named in reflection of the type locality of the taxon.

LONGUMNARIBUSSUIS SHIREENHOSERAE SP. NOV.

LSIDurn:lsid:zoobank.org:act:B00E3407-2F64-4EAE-9AF8-A92568705002

Holotype: A preserved specimen at the Natural History Museum, London, UK, specimen number NHMUK ZOO 1905.6.27.4 collected from Adampol, Turkey (Asia Minor), Latitude 41.1108 N., Longitude 29.2069 E.

This facility allows access to its holdings.

Diagnosis: The complex of species within the genus *Longumnaribussuis gen. nov.* has until now been treated as the species *Vipera ammodytes* (Linnaeus, 1758) *sensu lato*, but is sufficiently divergent from *Vipera* Laurenti, 1768, type species "*Vip. Redii* Latr" [=*Vipera aspis* (Linnaeus, 1758)] by subsequent designation of Fitzinger (1843) to warrant being placed within a separate genus, *Longumnaribussuis gen. nov.*.

Species in this genus are separated from all other Viperidae by the following unique combination of characters:

Head distinct from neck, crown covered with small scales, including frontal and parietal shields, these being sometimes quite large; eye moderate, with vertical pupil, separated from the 9-13 upper labials by two or three rows of small scales; nostrils lateral; nostril in a single or irregularly divided nasal which is separated from the rostral by a naso-rostral shield; rostral not deeper than broad. Supraocular shield large, bordering the eye but not extending posteriorly beyond the vertical of the posterior border of the eye.

Body cylindrical; scales keeled, with apical pits; scales in 21-23 rows (very rarely 19 or 25) ventrals rounded, 133-162 (both sexes). Tail short; 24-46 all divided subcaudals.

Most distinctive of all species in this genus is that the snout has an obvious horn-like appendage covered with 8 to 20 scales.

In the species *L. ammodytes* (Linnaeus, 1758), *L. steindachneri* (Werner, 1897), *L. connectens* (Bolkay, 1919) and *L. montenegroensis sp. nov.* the horn-like appendage points forward from the base, although in *L. connectens* (Bolkay, 1919) the angle is not as acute as in the other three species. In all the other species it points up at the base, although it may learn forward from part way up, or appear to lean forward in that from the rear, the angle down is not as acute as from the front.

Based on the preceding, the other eight species, some with newly named subspecies, in this genus, are as follows:

1/ *L. meridionalis* (Boulenger, 1903) with specimen BMNH 1898.3.30.27 collected from Athens as the type specimen and type locality, this species is confined to most of central mainland Greece, with a subspecies *L. meridionalis eviaensis subsp. nov.* on Evia Island to the immediate east.

2/ *L. montandoni* (Boulenger, 1904) with a type specimen from Greci, Romania, is confined to East Romania, Bulgaria, far north-east Greece and far north-west Turkey in the area adjoining the preceding countries.

3/ *L. epirusensis sp. nov*. with a centre of distribution in the Epirus region in South-west Greece, including the island of Corfu, which was shown to have a divergence of more than 8 MYA from nearest named relatives in the study of Roussos (2015). A divergent subspecies *L. epirusensis lefkadaensis subsp. nov*. occurs on the islands of Lefkada and Ithaki, south-west Greece.

4/ *L. maxhoseri sp. nov*. from the Peloponnese Region of south-west Greece which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015), that being *L. mariolisi sp. nov*..

5/ *L. mariolisi sp. nov*. from Kefalonia Island, south-west Greece, which was found to have a divergence of over 5 MYA from nearest relatives in the study of Roussos (2015).

6/ *L. buchholzi* from the Cyclades Islands, Greece (type locality Antiparos Island, South Cyclades), which was found to have a divergence of over 8 MYA from nearest relatives in the study of Roussos (2015). There are six additional subspecies of this nominate species formally named in this paper, each of the seven confined to one or more islands, generally separated from one another by historical sea depths in excess of 120 m, meaning separation during recent ice-age minima.

7/ *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey. Specimens from East Turkey, previously assigned to the same species, are a separate species formally named for the first time as *L. shireenhoserae sp. nov.*.

8/ *L. shireenhoserae sp. nov.* occurs in west Turkey, and was found to have a divergence of over 4 MYA from nearest relatives (that being *V. transcaucasiana*) in the study of Roussos (2015).

The preceding eight species are separated from one another by the following unique combinations of characters:

L. meridionalis has a horn-like appendage on the snout that is broader across and blunter at the top than in all other species. It also curls slightly backwards at the top. Iris beige to light yellow-orange. The pattern along the mid-dorsal line on the anterior and mid-body is of rounded-edged diamonds or triangles, an even chocolate brown in colour and without any obvious change at the edges or darkening. The wider parts of these diamonds or triangles are expanded in size so as to be as wide or wider than the dorsal area and expanding onto the upper flanks. These are joined at the tips on the midline, and/or sometimes narrowly separated. There are no markings in the upper labial area, save for a slight lightening of the posterior upper labials.

The subspecies *L. meridionalis eviaensis subsp. nov.* is the morphologically distinct subspecies of *V. meridionalis* from Evia Island, Greece. Roussos (2015) estimated a 3.6 MYA divergence from the type form of *V. meridionalis* from mainland Greece (Athens), which ordinarily would be more than sufficient for full species level recognition.

The subspecies *L. meridionalis eviaensis sp. nov.* from Evia Island, Greece is separated from the nominate form of *L. meridionalis* as follows.

L. meridionalis eviaensis sp. nov. has an extreme narrowing of the blotches running down the midline of the dorsum, combined with a reduction in their size. Notwithstanding this reduction, the blotches remain joined by lines of the same colour running between each blotch, which are in fact of similar thickness to the blotches themselves. The side blotches on the upper flanks are larger in size than the ones on the lower flanks, in contrast to what is seen in *L. meridionalis*, where the reverse is the case.

The contrast between the dark blotches and the lighter background colour is also much reduced in *L. meridionalis eviaensis sp. nov.* (light brown and dark brown, versus dark brown and whitish-grey), with both being of similar colour.

The side blotches are of similar intensity and contrast to those on the midline of the dorsum, versus not so in *L. meridionalis* where the mid dorsal blotches are bold and well marked, versus not so for the side blotches.

This gives the subspecies are very different appearance than that

of the nominate form.

There is no darkening of the edges of any blotches on either dorsum or sides in *L. meridionalis eviaensis sp. nov.*.

L. montandoni has a horn-like appendage on the snout that is narrow at the base and of similar thickness to the top and that is also of slightly smaller size than in most of the other species. The iris is light to dark brown in colour. The pattern along the mid-dorsal line on the anterior and mid-body is of diamonds that are of well-defined diamond-shape in turn joined by well defined straight lines of moderate thickness, this being a defining feature of this species. The diamonds and joining lines are of the same dark colour, usually either dark brown or orange, depending on the overall colouration of the snake. Upper and lower labials may be anywhere from unmarked to boldly marked or banded.

L. epirusensis sp. nov. has a horn-like appendage on the snout that is obviously broad at the base and pointed at the top, giving it a well-defined triangular shape, which also curls back slightly at the top. Diamonds on the back are moderately well-defined, (not as much so as in *L. montandoni*) and unlike that species, they tend to join directly as opposed to being joined by a straight dark line between them. They are of moderate width on the dorsum, but either not extending onto the flanks, or in specimens where they do, this is only just. Dark blotches along the midline are of an even colour and without noticeable darker etching on the outer edges (none at all in most specimens, barely noticeable in a few). Iris is beige to brown. Rear upper labials are white, forming the anterior part of a distinctive line running along the lower neck. Anterior labials are either unmarked are barred dark.

The subspecies *L. epirusensis lefkadaensis subsp. nov*. from Lefkada and Ithaki Islands, south-west Greece, was shown by Roussos (2015) to have diverged from nominate *L. epirusensis epirusensis subsp. nov*. with a centre of distribution in the Epirus region in South-west Greece some 4.31 MYA.

It is separated from nominate *L. epirusensis epirusensis subsp. nov*. by having moderately defined darkening at the edges of the merged dark blotches running down the spine of the body and heavily barred labials. Unique to this subspecies (when compared to all other subspecies or species in the genus) is that the dark side blotches on the anterior and mid body are both well-defined at the anterior edge and the posterior edge and in the form of well defined rectangles (length going up/down).

L. maxhoseri sp. nov. has a triangular-shaped horn-like appendage on the snout that curls forward slightly on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white. The dark blotches running down the spine are oval in shape (not triangular or diamonds), greatly expanded and join one another quite easily and across a decent section of the sides of each blotch. They are expanded in size so much that they expand down the upper flanks of the snake. On the upper body, they occupy an expanded area, meaning lighter areas are confined to being light beige intrusions into the otherwise mainly dark brown, reddish-brown or grey-brown upper surface. Head is light in colour, but heavily peppered dark.

L. mariolisi sp. nov. has a triangular-shaped horn-like appendage on the snout that does not curl forward or back on the upper half. White on the lower posterior labials is either dull, obscured or heavily peppered. Iris is orange-brown. The lower flanks are heavily flecked white, but the flecking is not distinct as seen in *L. maxhoseri sp. nov*.. The dark blotches running down the spine are oval in shape (not triangular or diamonds), but not greatly expanded as seen in *L. maxhoseri sp. nov*.. On the mid-body the dark oval markings are often separated (usually not the case in *L. maxhoseri sp. nov*., except sometimes down at the posterior of the body).

In *L. maxhoseri sp. nov*. the dark ovals on the dorsum have patches of semi-distinct black etching on each oval, whereas in *L. mariolisi sp. nov*. these ovals have a thin bold black line on the outer edge.

Side blotches are very distinct and well defined posteriorly, but not so anteriorly in *L. mariolisi sp. nov*. which is in contrast to *L. maxhoseri sp. nov*., *L. epirusensis sp. nov*., *L. montandoni*, *L. meridionalis* and *L. buchholzi.*

In *L. epirusensis lefkadaensis subsp. nov*. the side blotches are well defined both at the anterior and posterior edges and are in the form of well-defined rectangles (long side is up/down).

Head of *L. mariolisi sp. nov*. is an even orange-brown or grey in colour.

L. buchholzi of all seven subspecies, has the dark blotches running down the spine being reduced in width, or otherwise narrowed, meaning they are confined to the mid-dorsal line of body and not anywhere near the flanks. The blotches running down the spine are of irregular shape and do not conform to triangles, diamonds or ovals, rarely tending towards odd-shaped ovals, being joined by s-like markings of similar width, or sometimes as a line running down the spine with irregular edges in that they weave in and out on the outer edges. In almost all specimens of all subspecies, the blotches themselves and the intervening joins are also of irregular shape. The dark, usually orange-brown to chocolate brown blotches have slightly blackened outer edges, but not in the form of an obvious or well-defined boundary in any subspecies. In the three northern subspecies (north Cyclades), on the lighter part of the dorsum, but separate to the darker areas, are whitish flushes in parts near the darker edges, this being an important diagnostic character for these three subspecies. This is absent in the southern four subspecies (south/central Cyclades).

The four southern subspecies appear to be slightly smaller and more slender in average size and build.

The horn-like appendage on the snout in these four subspecies is long and thin and about the same length as the distance to the eye as measured from the posterior of the base.

L. buchholzi naxosensis subsp. nov. is separated from the other six subspecies of *L. buchholzi* (Cattaneo, 2021) as follows:

In *L. buchholzi naxosensis subsp. nov.* the posterior of the upper surface of the head, about where the venom glands are, is also flushed light, but without any obvious markings. The head itself is mainly one colour. The rear upper labials are tending white, turning to a line at the back of the head and onto the neck, but this is not distinct and obvious.

The scales of the horn-like appendage on the snout often has tiny raised tubercle like points. The upper part also usually points forward.

Iris is brown.

L. buchholzi naxosensis subsp. nov. is alone among the seven subspecies in that the upper flank is generally darker than the lower flank.

The six other subspecies of *L. buchholzi* are separated from *L. buchholzi naxosensis subsp. nov.* and all other species of *Longumnaribussuis gen. nov.* by the following unique combinations of characters as given below:

L. buchholzi mykonosensis subsp. nov. which occurs on the islands of Mykonos, Rinia and Tinos was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), some 2.3 MYA.

Along the midline of the dorsum of the body of *L. buchholzi mykonosensis subsp. nov.*, is a greyish brown line running more-or-less continuously for the length of the body. The appearance is of a collection of arrows joined to one another, but with the edges smoothed and rounded and with the pointed part of the arrow anterior and running to the base of the other arrow.

Only slightly lighter is the background colour elsewhere on the sides of the dorsum. Mid-flanks have indistinct darker brown blotches, while the background of the lower flanks becomes a more mustard yellow colour.

The contrasts between the colours in this subspecies is generally less than for all others from the Cyclades, giving the subspecies a generally drab and greyish-brown appearance. Exceptional to this, there is a bold white line running from the lower labials to the neck, with dark above, while the rest of the head is generally of one colour only. Iris is yellow-beige.

The horn-like appendage on the snout is longer than the distance from the appendage to the eye (measured from the posterior base), versus not so in the other two northern Cyclades subspecies.

L. buchholzi androsensis subsp. nov. from the island of Andros, was shown by Roussos (2015) to have diverged from *L. buchholzi sirosensis subsp. nov.* (type locality Siros Island, north Cyclades), and *L. buchholzi mykonosensis subsp. nov.* from the islands of Mykonos, Rinia and Tinos (type locality Mykonos) (north Cyclades)

some 3.58 MYA.

L. buchholzi androsensis subsp. nov. has a relatively thin, bold black edged wavy or ziz-zag line running down the spine along the neck and most of the body. Most of this line is fairly even in diameter, except for a small part of the mid-body where crude diamonds appear to be forming within the line and pushing out sections of the outer edge to make parts wider in a line that is otherwise mainly of the same thickness. The contrasting inner part of this mid-dorsal line is dark brown.

Most of the rest of the dorsum and flanks are an even light colour, usually whitish-grey, with side blotches either absent or faded to be merely sections of darker peppering on the posterior flanks.

A dark brown line runs from the snout, through the eye and posterior to it. Upper labials are slightly lighter than the lighter colour of the head above. The head anterior to the eyes and the crown have dark markings, behind of which is the commencement of a black line down the mid-dorsum of the neck, which in turn forms the black bordered line running the length of all or most of the body and tail. Iris is medium brown.

L. buchholzi naxosensis subsp. nov. from Naxos, Paros, Iraklia and Ios islands in the southern Cyclades (type locality Naxos) was estimated by Roussos (2015) to have diverged from the north Cyclades population (*L. buchholzi sirosensis subsp. nov.*, *L. buchholzi mykonosensis subsp. nov.* and *L. buchholzi androsensis subsp. nov.*) over 5 MYA. It was found by Roussos (2015) to have diverged from the other (described herein) southern Cyclades subspecies 2.57 MYA.

Characters unique to the subspecies *L. buchholzi naxosensis subsp. nov.* in addition to those previously mentioned are well defined dorsal markings in the form of brown coloured ovoid blotches on the neck, each well separated from one another by the lighter background area, but with each being joined by a thin brown line, this being so from the back of the head, all the way down the anterior body and down the main part of the snake. In line with all subspecies of *L. buchholzi subsp. nov*. these ovoid blotches are relatively small and reduced in size as compared to other species within *Longumnaribussuis gen. nov.*.

The lighter background colour of the dorsum and flanks is a whitish-grey.

A thin brownish-black line runs from the bottom of the eye to the back of the head. The side blotches are in the form of semi-distinct brown triangles. Iris is beige.

L. buchholzi sikinosensis subsp. nov. from Sikinos Island is a divergent form estimated to have diverged from nearest relatives 2.4 MYA by Roussos (2015).

L. buchholzi sikinosensis subsp. nov. is similar in most respects to *L. buchholzi naxosensis subsp. nov.* but separated from that taxon by the fact that the anterior blotches running down the midline of the dorsum are not connected by a thin brown line and the blotches themselves are medium brown in the centre rather than chocolate brown.

L. buchholzi sikinosensis subsp. nov. is further separated by its dull orange iris and the fact that a thick brown line runs from the bottom of the eye to the back of the head.

L. buchholzi koufonissiensis subsp. nov. from Koufonissi island was estimated to have diverged from nearest relatives 2.91 MYA by Roussos (2015).

Characters unique to the subspecies *L. buchholzi koufonissiensis subsp. nov.* in addition to those previously mentioned are dorsal markings of similar form to *L. buchholzi naxosensis subsp. nov.*, but being mainly black, as opposed to being mainly brown. The lighter part of the dorsum and flanks is so heavily peppered grey that it also appears to be a dark grey, rather than a whitish grey.

The white of the rear upper labials contrasts with the thick, well-defined black line that runs from the bottom of the eye to the back of the head. Iris is mainly dark brown.

L. buchholzi buchholzi (Cattaneo, 2021), defined herein as being from Antiparos and Despotiko islands in the south Cyclades only, (type locality Antiparos) was estimated to have diverged from nearest relatives 2.57 MYA by Roussos (2015).

Characters unique to the nominate subspecies *L. buchholzi buchholzi* (Cattaneo, 2021) in addition to those previously mentioned are the fact it is a generally orangeish coloured snake with a light whitish orange head, including front, sides and upper labials. A thick brown stripe runs from the rear of the eye to the back of the head.

Dorsally the midline consists of irregular orange-brown blotches with well defined black edges, mainly merged to form a continuum running along the spine. The contrasting orange-brown with well-defined black edges is similar in colouration to the oval blotches seen in typical type form *Daboia russelii* (Shaw and Nodder, 1797) from southern India. Brown coloured side blotches are squarish in shape, but somewhat irregular in shape and outline and overlain with a whitish-red wash making them only semi-distinct.

Unlike the other three south Cyclades subspecies, the horn-like appendage on the snout lacks dark pigment, speckling or peppering, and is instead generally light in colour. Iris is light yellowish-beige.

The two species *V. transcaucasiana* (Boulenger, 1913) with a type locality of Borzom, Georgia, confined to the region in Asia Minor, including Georgia and immediately adjacent parts of far western Turkey and *L. shireenhoserae sp. nov.* from East Turkey, previously assigned to the same species, are readily separated from all the preceding species by colour pattern on the dorsum.

The dark blotches running down the middle of the spine down the body are reduced in size and altered in shape.

In these two species the blotches are narrowed to form bands running across the dorsal surface, sometimes onto the flanks and sometimes not.

Each blotch has become in effect a narrow rectangle across the back (length running side to side).

The lighter grey areas of the dorsum therefore occupy a far greater area than is seen in all the other species. In both species the darker rectangular blotches are a dark greyish to black in colour and even in colour, there being no darkening at the edges or any obvious demarcation of the boundary with another colour or hue.

The head is of the lighter background colour with obvious heavy peppering or spotting.

Labials are generally not marked. Rarely there may be a grey or black spot on a labial on either side. There is no white rear labials or line running from there to the lower neck.

Iris is grey.

L. shireenhoserae sp. nov. and *L. transcaucasiana* are separated as follows.

The cross bands on the dorsum of *L. transcaucasiana* are widely spaced and separate from one another. There is no dark areas linking these bands or blotches.

By contrast in *L. shireenhoserae sp. nov*. these rectangles are slightly more expanded in the centres (on the dorsal midline) and sometimes, but not always connected to one another by a thin dark line of the same colour. There are no dark side blotches in *L. transcaucasiana* (rarely some dark peppering where the blotches would otherwise be), whereas there are semi-distinct side-blotches in *L. shireenhoserae sp. nov.*.

The lighter background colour of the dorsum of *L. transcaucasiana* is light whitish-grey, versus a medium to dark grey in *L. shireenhoserae sp. nov*..

L. transcaucasiana in life is depicted online at:
https://www.inaturalist.org/observations/117763482
and
https://www.inaturalist.org/observations/130076887
and
https://www.inaturalist.org/observations/15631414

L. shireenhoserae sp. nov. in life is depicted in Akkaya (2012) on page 184 at top and online at:
https://www.inaturalist.org/observations/60605411

For further images of the relevant taxa refer to the preceding formal description of *L. buchholzi sirosensis subsp. nov.*.

Distribution: *L. shireenhoserae sp. nov.* is restricted to the region of Istanbul, Turkey, east and south to at least the hills near the town of Bursa, Turkey, where it appears to be fairly common.

Etymology: *L. shireenhoserae sp. nov.* is named in honour of my wife Shireen Vanessa Hoser originally from Athlone, South Africa in recognition of her services and sacrifices to herpetology spanning some decades.

SUMMARY

With all 12 species as well as the relevant 8 newly named subspecies, subject to significant persecution by humans across their ranges, it is important that they each be recognized immediately and before any one of them becomes extinct through the misconception they are merely a part of a more common and widespread species as occurred in the example cited by Hoser (2019a, 2019b).

With a divergence from all other vipers estimated to be more than 15 MYA (Freitas *et al*. 2020), the new genus name for the group *Longumnaribussuis gen. nov*. formally proposed should be used to identify members of this distinctive group of vipers, again to further highlight their need to be conserved.

Because of the medical importance of these snakes, it is important that persons such as the notorious Wolfgang Wüster, or his subordinates, not be allowed to engage in taxonomic vandalism with respect of the various species and their names.

Besides adding to the conservation risks for the relevant taxa, the nomenclatural instability this would create may cause human lives to be threatened.

Refer to the relevant comments of Cogger (2014), Cotton (2014), Hawkeswood (2021), Hoser (1989, 1991, 1993, 1996, 2001a-b, 2007, 2009, 2012a-b, 2013, 2015a-f, 2017, 2019a-b), ICZN (1991, 2001, 2021) and Wellington (2015).

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CONFLICT OF INTEREST

None.