

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

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RAYMOND T. HOSER

LSIDurn:lsid:zoobank.org:author:F9D74EB5-CFB5-49A0-8C7C-9F993B8504AE

488 Park Road, Park Orchards, Victoria, 3134, Australia.

Phone: +61 3 9812 3322 Fax: 9812 3355 E-mail: snakeman (at) snakeman.com.au

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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*; *sikinosisensis*; *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 Ursebacher *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-Isailović *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), Fofopoulos *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), Gvozdencovic and Ikovic (2022), Gvozdík *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), Schweizer (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 195A1 (2) and 195AJ (a-b) and 195AQ(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 Sikinios 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):

Cycladi, Sporadi settentrionali, morfotipi, nuova sottospecie

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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 *Longunnaribussuis 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 *Krečák* (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 lean 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 lean 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 oscillate 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. connectens 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.

LSIDDurn: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 lean 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 a 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 or 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/vxnZtuOT3I/>

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>

<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 lean 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 a 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 or 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 *Longumnaribus suis 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.

LSIDDurn: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 lean 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. 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 a 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, Peloponnissos 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 lean 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.balkanica.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 lean 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 lean 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 a 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 or 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/vxnZtuOT3I/>
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. shirenhoserae 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:6876FBFA-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 lean 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 or 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, 1979) 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/vxnZtuOT3I/>

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/au/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.

LSIDDurn: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 lean 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 or 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 lean 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 a 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 or 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 *Longunmaribussuis 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.

LSIDDurn: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 lean 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 a 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 or 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 russellii* (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 lean 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 a 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 or 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.

LSIDDurn: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 lean 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 a 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 or 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 lean 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 or 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 *Longunmaribussuis 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 *Longunmaribus* 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, 1979) 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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Method: VISA MASTERCARD CASH CHEQUE OTHER
Amount: \$ _____
Card No.: _____
Name: _____
Date: _____
Expires: _____
CCY: _____

SUB-TOTAL \$604.54
G.S.T \$60.45
TOTAL \$664.99
AMOUNT DUE \$664.99

PRINT DESIGN SERVICE MARKETING

*see terms of trading for conditions of payment by other methods