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The Dice Snake, *Natrix tessellata* (Serpentes: Colubridae) in Pakistan: Analysis of its Range Limited to Few Valleys in the Western Karakoram

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Abstract.- Based on the recent rediscovery of a dice snake (*Natrix tessellata*) in the Karakoram mountains of north-central Pakistan (western Karakoram) and the only other records from northwestern Pakistan we utilize contemporaneous information on the ecology of *N. tessellata* and climate fluctuations during the Holocene to analyze its limited distribution to a few mountain valleys. We elaborate several plausible expansion routes from a glacial refugium in northern Afghanistan through the Hindu Kush Mountain Range into Pakistan and the western Karakoram. The apparent range restriction of *N. tessellata* to the mountains of northern Pakistan is discussed in regards to postglacial expansion speed and routes, available period during the Holocene, habitat requirement, competition with another semi-aquatic water snake, *Xenochrophis piscator,* and potential misidentification with the latter species.

Key words. *Natrix tessellata*, Colubridae, Ghizer Valley, Karakoram Range, postglacial refugia, competitive exclusion, *Xenochrophis piscator*, *Xenochrophis schnurrenbergeri*, dice snake.

INTRODUCTION

The dice snake (*Natrix tessellata*) is widely distributed from Germany to Italy in Europe, south to Egypt, and eastward through the Middle East and Russia to China and Afghanistan (Bannikov *et al*., 1971; Gruschwitz *et al*., 1999; Mebert, 2011a; Liu, *et al*., 2011). In Pakistan, *N. tessellata* has been reported only once from the northern Chitral Valley (Wall, 1911). Three dice snakes, two males and a female, were collected in 1910 at an altitude of about 6,000 feet" (~ 1,830 m) a.s.l. near the village Mastuj (Khyber Pakhtunkhwa Province). Wall (191:1932) noted that the species was plentiful "in a piece of ground adjoining a stream", likely referring to the numerous smaller ponds and streams found on the large alluvial plain formed by the Mastuj (= Kunar) and Yarkhoon rivers. However, Mastuj lies at 7,450 ft a.s.l. (~ 2270 m), and the river elevation of 6,000 ft. is not encountered until approximately 50 km downstream near the village Reshun. *N. tessellata* may occur at either locality, as both exhibit suitable habitat. However, we take the locality "Mastuj", as being the site where the specimens were collected despite the difference in altitude, as we suggest that elevation records were less accurate than naming of villages 100 years ago. Unfortunately, there are no voucher specimens, so re-examination of the Chitral dice snakes was not possible. Subsequent publications on the herpetofauna of Pakistan (Minton, 1966; Khan, 2002, 2006) and extensive surveys by the staff of the Pakistan Museum of Natural History in Gilgit-Baltistan, Cholistan desert and northern Khyber Pakhtunkhwa did not provide additional information on this species in Pakistan (see also: Baig, 2001; Baig *et al*., 2008; Khan, 2006; Masroor, 2011, 2012).

During a recent herpetological survey of wetlands by the Pakistan Wetlands Programme (PWP), WWF-Pakistan, the third author of this paper and other members of the WWF Pakistan regional office Gilgit-Baltistan, Pakistan, collected a single specimen of *N. tessellata* from Ghizer District, Gilgit-Baltistan. Basic data about this rediscovery were presented by Masroor and Mebert (2012), and the potential of population exchange between the historic Chitral records and the new locality was also investigated (Mebert and Masroor, 2013).

Herein, we analyze the range extension based

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on the newly found dice snake on a larger geographic scale by presenting factors that could restrict the distribution of *N. tessellata* to a few valleys in the Karakoram Mountain Range of northern Pakistan and explain the species' absence farther south. Relevant questions relate to temporal, structural or other abiotic factors that impede expansion of *N. tessellata* southward. Are there also biotic factors responsible for this range restriction?

MATERIALS AND METHODS

The new specimen of *Natrix tessellata* was collected on the 20 August 2011 in the Gahkuch Wetlands Complex adjacent to the Gilgit (or Ghizer) River, Gilgit-Baltistan, Pakistan, at an elevation of 1,845 m a.s.l. (Fig. 1A, and Masroor and Mebert, 2012). The wetlands consist of sandy-stony soil with dense coverage of grasses and bushes across an area of 130.76 hectares (Fig. 1B). Photos of the new specimen were taken in the field (Fig. 1C), depicting dorsal, ventral, and lateral views of the head. The specimen was preserved in 40% formalin at Pakistan Museum of Natural History as PMNH No. 2478. The snout-vent length and tail length were measured with a digital calliper to the nearest 0.1 mm. Table 1 lists features of scalation, including the number of ventral, subcaudal, labial and ocular scales, dorsal scale rows and definitions of measuring methods.

Comparative material was acquired through museum collections, literature data, and private persons. Following museum acronyms are used in the text: CAS (California Academy of Sciences, USA), FMNH (Field Museum of Natural History, USA), NHMW (Naturhistorisches Museum Wien, Austria), PMNH (Pakistan Museum of Natural History, Pakistan), ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Germany), ZMUC (Zoological Museum of the University of Copenhagen, Denmark), UF (University of Florida, Florida Museum of Natural History, USA).

Applications of Google Earth (version 6.1, 2011) and literature accounts were used to isolate possible dispersal routes and locate a potential glacial refugium based on our knowledge of preferred habitats and regional elevation limits of *N. tessellata* (see refs. In Mebert, 2011a). Most locality names in the text were taken from Google Earth or Google Maps (= GE, GM) labels, including those not depicted in figures here due to space limitations and decreased resolution on our maps. Hence, sites not depicted can be located in GE or GM.

RESULTS AND DISCUSSION

The collection of *Natrix tessellata* from Gahkuch, Ghizer River, in the Karakoram Range represents the second known locality for this species in Pakistan. The earlier record from near Mastuj, Chitral Valley (Wall, 1911) is separated from the new locality by approximately 170 km of river valleys and one high elevation pass > 3,700 m a.s.l. with currently unsuitable habitat. However, imagery data and the most recent available ecological information available on *N. tessellata* show that suitable habitat for the species occurs along most rivers in the northern third of Pakistan when compared to similar mountain valleys inhabited by this species from the Caucasus region to Central Asia (see refs. in Mebert, 2011a). *Natrix tessellata* also occurs in lowland and heavily irrigated river systems elsewhere, such as the Euphrates River in Iraq and the Nile River and Suez Canal area in Egypt (Baha-El-Din, 2011; Ibrahim, 2012). However, dice snakes do not occur in similarly structured broad alluvial systems south of the Karakoram Range, such as those found along the lower Kabul, Dir and Indus rivers. Whereas, the distribution of *N. tessellata* in Pakistan can be attributed to dispersal during favorable climatic periods in the Holocene (Mebert and Masroor, 2013), the lack of dice snakes south of the Karakoram Range along the Indus River and its tributaries is enigmatic.

We analyze four possible scenarios that may explain the apparent lack of dice snakes in suitable habitats south of the western Karakoram Range. First, we analyze whether *N. tessellata* had sufficient time to disperse into the Swat Valley and more eastern valleys from a potential glacial refugium in the southern Turanian lowlands (far northern Afghanistan and adjacent areas). Second, we briefly look at the habitat suitability for *N. tessellata* south of the western Karakoram Range

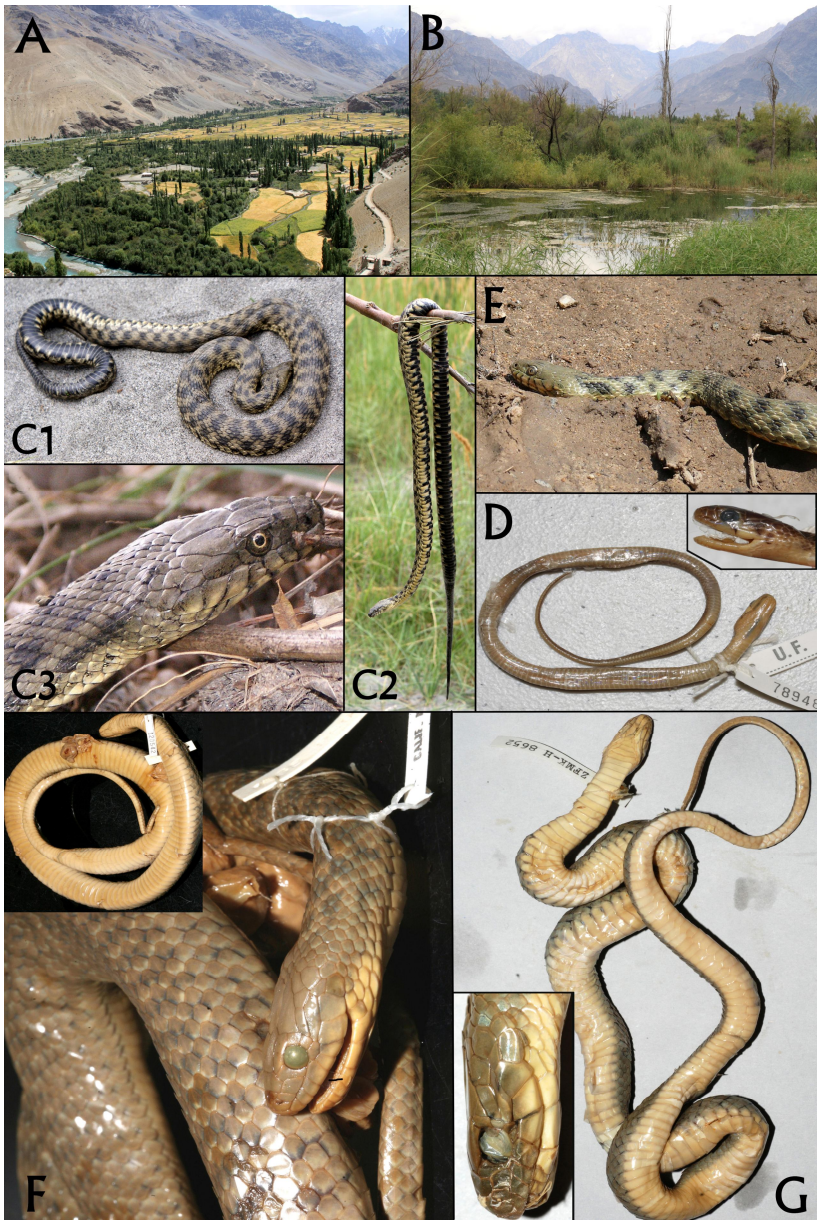

Fig. 1. Pictures relating to dice snakes (*Natrix tessellata*), checkered keelbacks (*Xenochrophis piscator*) and habitats from Pakistan (**A-D**) and Afghanistan (**E-G**); **A:** Karakoram valley at Gahkuch Ghizer Distct, Gilgit-Baltistan, Pakistan, where the dice snake was rediscovered and collected at the edge of the wetland along the right side of the image; **B:** Lentic habitat in the Gakhuch Wetland Complex; **C**: dorsal (C1), ventral (C2) and lateral (C3) head views of the dice snake collected from Gahkuch Wetlands Complex; **D:** Checkered keelback, *Xenochrophis piscator*, (UF 78948) from Peshawar, Khyber Pakhtunkwha Province, Pakistan. Whereas dorsal color pattern can be quite similar between both water snake taxa, the unmarked venter of *X. piscator* is clearly distinct from the black and white ventral pattern typical for *N. tessellata* (see Fig. 1C2). Photo courtesy of KENNETH L. KRYSKO; **E**: Dice snake, *Natrix tessellata*, from Kunduz, Afghanistan, 30. April, 2010, approx. 450 m a.s.l. Photo and copyright by FRANK JOISTEN; **F:** Checkered keelback, *X. piscator*, (CAS 120542) from 40 km SW of Jalalabad, Nangarhar Province, Afghanistan. Photo courtesy JENS V. VINDUM; **G**: *X. piscator* (ZFMK-H 8652 and labelled as *X. sanctijohannis*, but see text), Jalalabad, Nangarhar Province, Afghanistan. Photo courtesy GERNOT VOGEL.

Table 1.- Morphological data of *Natrix tessellata* and *Xenochrophis piscator* from Pakistan: SVL (from tip of snout to vent in mm), TL (from vent to tip of tail in mm), ventrals according to DOWLING (1951), subcaudals in pairs, DORS1, 2, 3 (number of dorsal scale rows at the 20th ventral scale, at mid-ventral position, and at the 5th ventral scale prior to the anal scale).

Characters	PMNH 2478	PMNH 2240	PMNH 1312	PMNH 1895	PMNH 1975	PMNH 2033	PMNH 1506
Locality	Gahkuch, Ghizer Dist., Gilgit-Baltistan	Jubho Lagoon, Badin, Sindh	Bahawalpur, Punjab	Shakarparian, Islamabad	Shakarparian, Islamabad	Chotiari reservoir, Sanghar	Islamia University, Bahawalpur
Species	*N. tessellata*	*X. piscator*	*X. piscator*	*X. piscator*	*X. piscator*	*X. piscator*	*X. piscator*
Gender	Female	Female	Female	Female	Male	Male	Male
SVL	870	935	910	770	430	660	500
TL	205	360	310	315	180	175	250
ventrals	176	150	152	153	140	145	142
subcaudals	61	85	82	87	76	43-tail incomplete	92
infralabials	9-10	10	9-10	10	9	9	9-10
supralabials	8	9	9	8-9	8	8	8
preoculars	2	1	1	1	1	1	1
postoculars	4	3	2	3	3	3	4
DORS1	19	19	19	19	19	19	19
DORS2	19	19	19	19	19	19	19
DORS3	17	17	17	17	17	17	17

(Hindu Kush-Karakoram mountains) and the Indus River alluvial plains. Thirdly, we diagnose another semi-aquatic snake, *Xenochrophis piscator*, which may be confused for the dice snake. And finally, we explore whether *N. tessellata* may be competitively excluded by *X. piscator* from the southern versant of the western Karakoram and areas farther south in Pakistan.

First scenario – time for expansion was insufficient

Expansion speed

Lack of distribution data of *Natrix tessellata* from the past and present for most of Pakistan, as well as lack of research on dispersal rate, prevent any concrete proposition on the expansion speed of peripheral populations of dice snakes. However, there is plenty of information on the biology of *N. tessellata* and paleobiogeographic scenarios from European reptiles to deduce approximate expansion rates for this species.

First, phylogeographic analysis on dice snakes (Guicking *et al*., 2004, 2009; Guicking and Joger, 2011; Marosi *et al*., 2012) indicate that they survived in only one or perhaps a few glacial refugia in southeastern Europe or in Turkey, where suitable climatic conditions persisted during glacial periods (Hewitt, 1999). With the onset of a warmer climate, a postglacial range expansion followed rapidly along the river system of the Danube and Rhine northward into central Europe, as identical haplotypes in dice snakes from Bulgaria and western Germany indicate (Guicking and Joger, 2011). Complementary biogeographic analyses on northern and isolated populations of *N. tessellata* in the Ukraine and Russia (Kotenko *et al*., 2011; Litvinov *et al*., 2011; Ratnikov and Mebert, 2011), comparative genetic results for that region (Marosi *et al*., 2012), and Holocene fossil records of *N. tessellata* from the upper Danube valley (Markert, 1976) provide further support for the rapid postglacial range expansion scenario.

Second, comparative studies show that by 8 ka BP, temperatures in all seasons had recovered across Central Europe to values within 1.0°C of current temperature values with a peak around 6 ka BP (Davis *et al*., 2003), whereas temperatures farther south in Europe were suitable for dice snakes

during the entire mid-Holocene Climatic Optimum (= the Atlantic period) from 9 to 5 ka BP. This provides European *N. tessellata* 2,000–4,000 years to expand from glacial refugia to their northern and currently isolated sites in central Germany.

Third, to assess the expansion distance for dice snakes to reach the central German sites, we take two likely glacial refugia based on low lying fluvial areas in southeastern Europe, (a) around Belgrade, Serbia, at the southern end of the Pannonian Plain, and (b) the plain around Skopje, northern Macedonia. The corresponding expansion distances along the Morava, Danube and Rhine rivers cover 1,500 km from refugia (a), and 2,000 km from refugia (b) respectively. Consequently, the expansion rate varies between ~ 400–1000 meters/year. This value is quite similar to the calculated minimum dispersal rate of 500 m/year for another semi-aquatic, sympatric and thermophilic reptile species, the European pond turtle, *Emys orbicularis*, after its arrival in northern Europe (Sommer *et al.*, 2007, 2011). Radiotelemetric studies on *N. tessellata* show that individuals do move distances of this magnitude along shore habitat within one year or season (Conelli *et al.*, 2011; Velenský *et al.*, 2011). Although these latter studies show the potential straight line movement within a habitat and season, they do not necessarily represent a dispersal rate, which is a behaviour virtually impossible to observe today. However, numerous studies show that *N. tessellata* can quickly colonize sites with newly created suitable habitat, where no dice snakes have been observed for years (Strugariu *et al.*, 2011; Velenský *et al.*, 2011), probably reflecting a barely observable constant dispersal from nearby populations. In addition, dice snakes are particularly successful colonizers and can develop large populations within a few years after dispersal into a new, suitable site (Mazza *et al.*, 2011; Mebert, 2011b; Bendel, 1997; Velenský *et al.*, 2011).

Glacial refugia

Relating above scenario from Europe to the southeastern range limit of *N. tessellata* in central Asia, we suggest that either the glacial refugia of *N. tessellata* or its initial dispersal point in the early stages of the Holocene (Preboreal 10 to 9 ka to Boreal 9 to 8 ka BP) was located in the southern Turanian lowlands (Afghanistan, Turkmenistan, Uzbekistan, Tajikistan, see Fig. 2), including the Kyzi Kum and Kara Kum deserts, and the Ustyurt Plateau; this refugial area was bordered by the Caspian Sea to the west, the Pamir and Tien Shan mountains in the east, and the Hindu Kush (*sensu lato*) and Kopet Dagh mountains in the south. The southern Caspian Sea likely had a moderating effect on the regional climate (Tarasov *et al.*, 2000). From these refugia in the southern Turanian lowlands, post-glacial colonization likely followed the Amu-Panj River system, which consists of vast alluvial plains, reaching to northern Afghanistan and adjacent areas, and thus, paralleling dispersal events of the dice snake suggested for regions west and north of the Caspian Sea (Guicking *et al.*, 2004, 2009; Guicking and Joger, 2011).

To take a conservative approach, we consider the lowlands up to around 500 m a.s.l. (~ green shaded area in Fig. 2) as suitable for survival or population dispersal during the cooler stages of the early Holocene. Thus, *N. tessellata* likely occurred at Kunduz and Baghlan (60 km south of Kunduz) in Afghanistan, and also Moskovskiy and Kulob in Tajikistan (see Fig. 2). A recent photo of a dice snake from Kunduz at about 400 m a.s.l. (Fig. 1E) confirms its existence at that site. Bill (2010) and J. Ševčik (pers. comm.) also report that the dice snake is common in the reed vegetation in nearby southwestern Tajikistan, *e.g.*, in the springs of Čilučor-Čašma (Chilu Chor Chashma) at Šartuz (= Shahrtuz) 100 km northwest of Kunduz. Various multidisciplinary data show, that the Turanian lowland, as well as the steppes of Kazakhstan further north, was more humid and had more vegetation during the beginning of the Holocene than today (Lioubimtseva and Cole, 2004; Beer *et al.*, 2008 and refs. therein). The maximum of these climatic conditions occurred about 6 ka BP, about the same time warmer climate has been reported across most of central and northern Eurasia, at which time followed a drier climate.

Expansion through Hindu Kush mountains

With additional climate warming and aridification in the Atlantic period (~ 9 to 5 ka BP),

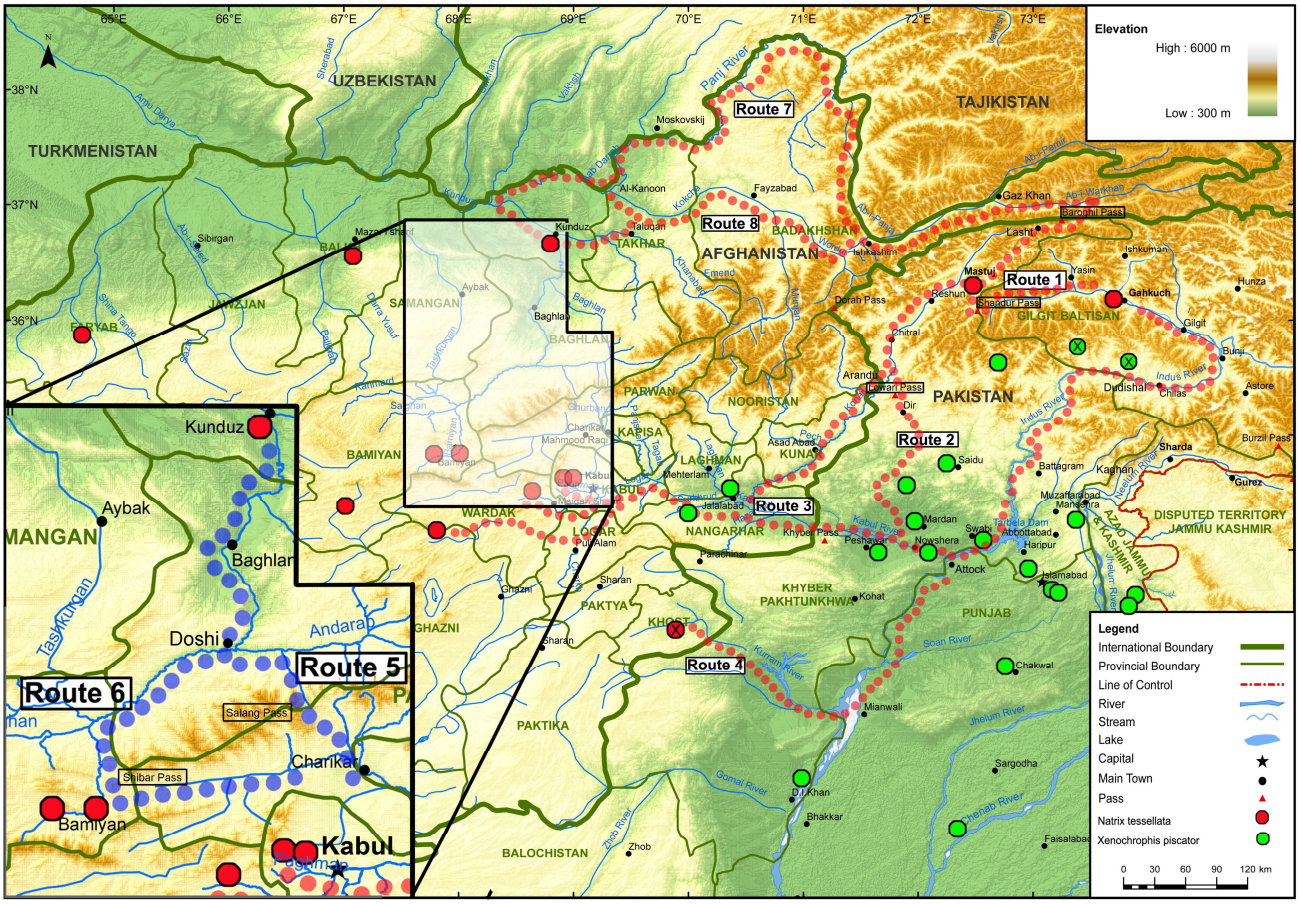

Fig. 2. Map of proposed expansion routes (light red dots) of *Natrix tessellata* to reach the Gahkuch site in Pakistan. Route 1: from Mastuj in northwestern Pakistan via Shandur Pass into Ghizer Valley; Route 2: from Mastuj farther downstream passing Chitral and upstream a sidevalley over the Lowari Pass, and continuing downstream into Dir Valley and Kabul River (for a closer view of routes 1 and 2 see also Mebert and Masroor 2013); Route 3: from Jalalabad, Afghanistan, along Kabul River into Pakistan; Route 4: form Khost, Afghanistan, along Kurram River into Pakistan. In routes 2–4, expanding dice snakes would reach the Indus Rivers, and subsequently expand upstream as far as Gahkuch. Due to the lack of a voucher specimen or photo identification for *N. tessellata* from the Khost area, that locality (red dot) is marked with an X. Also displayed are records of *Xenochrophis piscator* (green dots, including two marked with X to represent non-expert identification). See text for further explanations. Green shaded area in the upper left of the map represents the southern Turanian lowlands, regarded as likely glacial refugia for *N. tessellata*, from where postglacial expansion routes followed through the Hindu Kush Mountains southwards to the alluvial plains at Bamiyan and the Kabul plateau (enlargement lower left with Route 5 and Route 6 marked with blue dots), and eastwards into Pakistan (routes 7 and 8 in red dots). Also shown are river routes from known sites of *N. tessellata* in Wardak and Kabul provinces eastwards to connect with Route 3 in Jalalabad, from where only two *X. piscator* vouchers are known (green dots).

N. tessellata dispersed further east- and southward to colonize suitable valleys of the Hindu Kush mountains. Dispersal continued over some mountain passes to open areas, such as the alluvial plains near Bamyian and the greater Kabul area in Afghanistan, areas currently occupied by *N. tessellata* (Fig. 2 and vouchers in the Table II). For example, there are two likely routes from Baghlan (Kunduz region) through the Hindu Kush to Jabal-os-Saraj and Charikar, 60 km north of Kabul and represent the northern border of the large plateau and various alluvial plains in the greater Kabul area. The first

proposed route (Route 5 in Fig. 2) includes a distance of 170 km from Baghlan upstream along the Kunduz River to Doshi, east and up the northern Salang Valley, over the Salang (or Koashan) Pass at 3,800 m a.s.l., and down the southern Salang Valley onto the plains north of Kabul. A second proposed route (Route 6 in Fig. 2) takes 320 km from Baghlan to Doshi, then west upstream the Kunduz River to Doab-Mikh Zarrin, south into the side valley to Darreh-ye-Jalmesh (Ghandak ancient fortress), further to Bariki (Bamiyan area), then west over the Shibar Pass at 2,930 m a.s.l., and down the eastern Bamiyan Valley to the plains north of Kabul.

Table II.- Comparative material included.

Natrix tessellata

CAS 115972: Paghman, Kabul Province, Afghanistan, ~ 2,440 m a.s.l., 11–12 July 1965, W. S. STREET.

FMNH 161112: Mazar-i-Sharif, Balkh Province, Afghanistan, ~ 830 m a.s.l., 1–3 Sept 1965, W. S. & J. K .STREET.

FMNH 161179 and -80: 2 specs., Paghman, Kabul Province, Afghanistan, ~ 2,250 m a.s.l., 11–12 July 1965, W. S. STREET.

FMNH 161204: Maimana, Faryab Province, Afghanistan, ~ 897 m a.s.l., 7 Sept 1965, W. S. STREET.

NHMW 34780: Bamian, Bamyan Province, Afghanistan, ~ 2,500 m a.s.l., 16 July 1968, MR. BAUMGARTNER

Non-vouchered: Sahr-i-Zohak, Bamyan Province, Afghanistan, ~ 2,450 m a.s.l., caught in a plant field of alfalfa and released, 1974, H. SEUFER (pers. comm.)

ZFMK 14542–44: 3 specs., Jalriz, Sanghlak (Maidan), Wardak Province, Afghanistan, 2,400 m a.s.l., 31 March 1974, H. SEUFER.

ZMUC R60100: Sar-i-Chiasma, Koh-i-Baba Mts., sw. of Kabul, near Jalriz and Jalez, Wardak Province Afghanistan, ~ 2,370 m a.s.l., 1948, N. HAARLOEV.

ZMUC R60101: Panjao, Koh-i-Baba Mts., Bamyan Province, Afghanistan, 28 July 1948, 2,720 m a.s.l., N. HAARLOEV

Xenochrophis piscator

CAS 120542: 40 km SW of Jalalabad, Nangarhar Province, Afghanistan, , ~ 1050 m a.s.l., 7 May 1968, R. J. CLARK and E. D. CLARK.

PMNH 115: Chotiari Reservoir, Sanghar, Sindh Province, Pakistan

PMNH 371: Khanpur Dam, Khyber Pakhtunkhwa Province, Pakistan

PMNH 941: Rawal Dam (foothills of mountains), Islamabad Capital Territory, Pakistan

PMNH 1312: Baghdad-i-Jadid Campus, Islamia University, Bahawalpur, Punjab Province, Pakistan

PMNH 1506: Marot, Bahawalnagar, Punjab Province, Pakistan

PMNH 1724: Chak T-56, Rahimyar Khan, Punjab Province, Pakistan

PMNH 1895: Shakarparian, Islamabad Capital Territory, Pakistan

UF 78948: Peshawar, Pakistan, Khyber Pakhtunkwha Province, Pakistan

ZFMK-H 8652: Jalalabad, Nangarhar Province, ~ 570 m a.s.l., Afghanistan

Alternatively, a general aridification since 6.3 ka BP (Campo and Gasse, 1993; Gasse *et al*., 1996; Miehe *et al*., 2002) likely was responsible for a decrease in forest cover in the Himalaya/Tibet region, which in turn allowed the increase of solar radiation reaching directly the surface, and thus, additionally heating up rocky/stony lake and river shores and slopes commonly used for thermoregulation by dice snakes. This enabled *N. tessellata* to occupy sites in quite cool, arid areas, as is exemplified in the treeless Lar Valley at 2,700 m a.s.l. of Iran today (Rajabizadeh *et al*., 2011).

Expansion into Pakistan and western Karakoram Range

Since there are no dice snakes in southern Pakistan, an expansion from Iranian populations into Pakistan is being excluded *a priori*, likely as a consequence of high aridity in the greater Iranian-Pakistani border region. For postglacial *N. tessellata* to reach the Mastuj site in the Chitral Valley of northwestern Pakistan, we suggest two northern routes (Routes 7 and 8 in Fig. 2). Both routes begin in the Turanian lowlands in northern Afghanistan, converge at Ishkashim at the Tajikistan-Afghanistan border (2,640 m a.s.l.), and continue as one route from there (see below). Dice snakes from the region around Kunduz could have reached the Kokcha River via Taloqan (= Taluqan) and Hezar Bagh or the Amu-Panj (Pjanzh or Ab-i-Panja) River from Kunduz downstream (row of reddish dots connecting Taluqan-Kunduz-Moskovskij in Fig. 2). These snakes could have served a source populations for two routes into Pakistan elaborated below.

The first route (Route 7) of 720 km begins at Moskovskij, Tajikistan, the easternmost town of the Turanian lowlands at the Panj River. It follows along this Tajik-Afghan border riverupstream to Ishkashim. From there, the route continues eastward into the Wakhan Corridor, the Afghan valley

bordered by Tajikistan and Pakistan, follows upstream to Gaz Khan (~ 2,800 m a.s.l.), and up to Patukh (3,260 m a.s.l.) in the far northeastern corner of Afghanistan. From Patukh, *N. tessellata* expanded another 25 km upstream and over the Baroghil (or Broghol) Pass at 3,800 m a.s.l. into Yarkhoon Valley, Chitral District, Pakistan, and continue downstream to Lasht at 3,000 m a.s.l. This locality is 75 km upstream from Mastuj and can be regarded at the relevant point to be reached before climate had cooled to current levels, rendering high-elevation sites unsuitable for *N. tessellata*.

A second route (Route 8) begins at Al-Kanoon (confluence of the Kokcha and the Panj Amu rivers), leads upstream along Kokcha River to Fayzabad and Baharak into an eastern branch of the Kokcha River to Zebak and over the pass near Bazgir at 3,060 m a.s.l., down to Ishkashim. From there Route 8 conjoins Route 7 to continue jointly to Lasht in Pakistan. The total distance covered by dice snakes along Route 8 is at least 560 km. The river systems involved in Routes 7 and 8 may not provide suitable habitat for dice snakes along their entire lengths today due to lack of foraging grounds based on strong currents and turbidity or lack of microstructure along their banks. But these rivers may have provided sufficiently suitable habitat for colonization and expansion throughout various periods during the frequent fluctuations of climates, vegetation, landscapes, and associated biodiversity throughout the Holocene.

In conclusion and according to the various literature data and wealth of recently compiled biological information on *N. tessellata* (Mebert, 2011a), we suggest that the time span during the Holocene Climatic Optimum was sufficient for the dice snake populations of the southern Turanian lowland to reach the Pakistani sites at Mastuj and Gahkuch. In order to advance to these sites, *N. tessellata* must have colonized and overcome high passes of 3,000–4,000 m a.s.l. in Pakistan (Broghol, Shandur, Lowari) latest at the end of the warm Atlantic period (6 to 5 ka BP). The subsequent cooling climate probably was easily avoided by colonizing rivers downstream that experience moderate to optimal climate. Consequently, *N. tessellata* had 5,000–6,000 years to reach all areas along the Indus River systems and associated lowlands from northern to southern Pakistan, approximately 1,000–2,000 km downstream. The resulting dispersal rate of 150–400 m per year is smaller (or slower) than estimated for a postglacial expansion of *N. tessellata* into Central Europe (see above), but remains in the same magnitude. However, since there are no *N. tessellata* in central or southern Pakistan today, the hypothesis of "insufficient time" to expand along the Indus appears as unlikely cause to explain its current range restriction.

A final alternative scenario might be posed. If Pakistani *N. tessellata* represent a relict from the previous Eemian (or Mikulin) interglacial (approx. 114 to 131 ka BP), when during warmer periods north of the Alps temperatures were 1–2°C higher than today, but 1–2°C cooler south of Alps (Kaspar *et al.*, 2005). Only genetic data could resolve this issue. Notwithstanding, the expansion routes would have remained the same as those used during the Holocene Climatic Optimum.

Second scenario – habitat is unsuitable throughout most of Pakistan

Is the habitat between the southern valleys of the western Karakoram Range and the alluvial plains of the Indus River unsuitable for *Natrix tessellata*? Regarding the broad range of habitats, in which *N. tessellata* is thriving today (Mebert, 2011a), this hypothesis appears not plausible to explain its absence in most of Pakistan. The dice snake is one of the few snake species that has colonized three continents, ranging from central Europe to Egypt in Africa, and as far east as Xinjiang Province in northwestern China, Asia (Mebert, 2011a). Suitable habitats include exposed banks on forested alluvial plains and along rivers in deep mountain valleys of temperate to southern Europe, the desert oases of Jordan, Syria and Iran, flood plains in the semi-arid steppes of central Asia, freshwater lakes, brackish and marine habitats in the Mediterranean, Black and Caspian seas, and aquatic habitats in treeless mountain valleys above 2,000 m a.s.l. in the South of western and central Asia. Rocky shores, whether natural or anthropogenic (*e.g.*, rip-raps), are particularly preferred, as can be found downstream from the village Attock (near the Indus-Kabul rivers confluence, Punjab Province,

Pakistan) with variable riparian microstructure of soil and rocks, along the broad Indus River southward through hilly country into central Pakistan (see comparable conditions in Mebert *et al*., 2011; Velenský *et al*., 2011). Furthermore, large reedy areas on calm lakes and rivers, as well as low current irrigation systems are inhabited, mostly in southern lowlands, *e.g*., along the Nile, Euphrates, and Tigris rivers (more examples in Baha-el-Din, 2011; Mebert, 2011a). This habitat type is also provided by the Indus River, as it widens substantially farther downstream at Kalabagh, leading into vast lentic (quiet) systems with many irrigation channels. At present, we can not recognize any structural habitat elements along the Indus alluvial plain that would preclude the presence of *N. tessellata*.

Other habitat related factors may temporarily inhibit further expansion along the Indus River, such as increased water current, thus reducing the successful capture of fish, the principal prey of dice snakes. However, fish is probably readily available in the lentic systems associated with the Indus River. Other semi-aquatic, fish-eating snakes like *Xenochrophis piscator* occur in that area (Khan, 2002). Furthermore, the stomach contents of one of the specimens collected by Wall (1911) had swallowed a large newt, indicating that the dice snake diet is not limited to fishes in Pakistan, similar to accounts from other Asian parts of its range (see refs. in Gruschwitz *et al*., 1999; and in Mebert 2011a).

Third scenario – Records of Xenochrophis piscator *in Northern Pakistan may represent misidentified* Natrix tessellata

In central to southern Pakistan, east of the Indus River, *Xenochrophis piscator* and the similar *X. schnurrenbergeri* are sympatric, the latter only recently elevated to species status (Vogel and David, 2007, 2012; Purkayastha *et al*., 2010; Dubey *et al*., 2012). These taxa have often been confused and are separated by minor, but consistent, external characters (nuchal mark, ventral color pattern, some pholidosis characters), and thus, are treated as one entity for the purpose of distinguishing both taxa from *N. tessellata* concerning Pakistani specimens. From limited data available, *X. schnurrenbergeri* has been confirmed for Pakistan based on two vouchers from Thatta and Mirpur Sakro, Sindh Province, southeastern Pakistan (Vogel and David, 2007, 2012). The few habitat and locality data available show that *X. schnurrenbergeri* has been found only in lentic (slow moving to standing) aquatic systems of lowlands at elevations < 200 m a.s.l. (Kramer, 1977; Mohapatra *et al*., 2010; Purkayastha *et al*., 2010; Vogel and David, 2012).

Although, *X. schnurrenbergeri* is currently not known from any locality near the recently discovered *N. tessellata* localities in northern Pakistan, based on the available ecological and distribution information, we anticipate its occurrence in the large and low lying lentic system of five large rivers in the Punjab Province of Pakistan. Equivalent habitat for *X. schnurrenbergeri* occurs to the northern margins of the Jhelum River, only 350 km (straight line) south of the *N. tessellata* site at Gahkuch and only 150 km south of Tarbela Dam, where the Indus River exits the Himalaya foothills. Due to the lack of sampling in this area and farther north in Pakistan and the existence of suitable habitat in relative proximity, we can not yet exclude the occurrence of *X. schnurrenbergeri* in northern Pakistan. For this reason and the potential of confusion between both *Xenochrophis* to each other we combine them to analyze potential misidentification with *N. tessellata* for watersnake records from northern Pakistan.

Numerous photographs of *X. piscator/ schnurrenbergeri* show that some specimens are superficially quite similar to *N. tessellata* in color pattern (*e.g.*, Fig. 97 in Khan, 2002, and website-pictures of *X. piscator/schnurrenbergeri* in http://cspt.in/index.php, http://reptiledatabase. reptarium. cz/, siamreptile.com, animalrescuesquadgoa.com, or snakesoftaiwan.com). This may increase the chance of misidentification of *Xenochrophis* spp. with *N. tessellata* for watersnakes from northern Pakistan, in particular where only visually sighted specimens were taken to delineate range limits. However, at a closer look, *X. piscator/schnurrenbergeri* can be well distinguished from *N. tessellata* based on a combination of scalation characters and color pattern. According to Minton (1966), Khan (2002, 2006), Vogel and David (2007, 2012), Purkayastha *et al*. (2010), personal observation, as well as data

presented in Table 1, we provide the following list of characters with which to distinguish *N. tessellata* from *X. piscator*/*schnurrenbergeri* in Pakistan and Afghanistan

1. No. of ventrals (independent of sexual dimorphic differences): > 170 in *N. tessellata*, with the lowest value of 172 counted for a specimen from Paghman, Afghanistan, and < 160 in *X. piscator/ schnurrenbergeri*, with the highest value found at 153 for a specimen from Islamabad, see Tab. 1, or 159 (Khan, 1984) for a female of the "*sanctijohannis*" morph of *X. piscator* (see comments to this morph in VOGEL and DAVID, 2012).
2. No. of temporals touching postoculars: 1 in *N. tessellata*, usually 2 in *X. piscator/schnurrenbergeri.*
3. No. of preocular scales (including suboculars): 2-3 in *N. tessellata*, 1 in *X. piscator/schnurrenbergeri.*
4. Presence of two dark slim streaks laterally on the head: none in *N. tessellata*, but two streaks in most *X. piscator* and in all *X. schnurrenbergeri*, with one postocular streak from eye to the last two supralabials and a subocular streak to the 6. and 7. supralabial.
5. No. of supralabials: normally 8 in *N. tessellata*, and 9-10 in *X. piscator/schnurrenbergeri*.
6. Ventral pattern: *N. tessellata* usually exhibits a heavily "black and white marked" venter, whereby the pattern often resembles a chessboard on the anterior body with the black portion increasing in size towards the tail. *X. piscator* usually exhibits a whitish venter with virtually no dark ventral pattern except for some darkening on the outermost edges. In *X. schnurrenbergeri* the ventral and subcaudal scales exhibit a broad, dark margin.

These characters represent consistent, diagnostic differences between *X. piscator* and *X. schnurrenbergeri* on one side and *N. tessellata* on the other side. The external differences are easy to check in freshly captured specimens and enable quick species identification. Therefore, we presume the correct identification of sighted *X. piscator* from northern Pakistan, at least of those field observations provided to us by snake experts, including the specimen from Kalam in the Swat Valley observed by Muhammad Sharif Khan (pers. comm.).

Fourth scenario – competitive exclusion by X. piscator

One potential cause for a barrier effect to the southward expansion of *N. tessellata* in Pakistan may result from an interspecific competition with the ecologically most similar semi-aquatic snake species in Pakistan, the ubiquitous checkered keelback, *Xenochrophis piscator*, whereas *X. schnurrenbergeri's* restriction to lentic systems (Vogel and David, 2012; Purkayastha *et al.*, 2010) renders it less comparable to dice snakes. *X. piscator* is the most common water snake species from the upper to the lower Indus River system, principally occurring throughout southern and central Pakistan. It occurs north up to the south-facing versant of western Himalaya and missing only in the deep valleys of the Hind Kush and Karakoram mountains, from where *N. tessellata* is known (Khan, 2002; Masroor, 2012). Hence, they have an approximate parapatric distribution in northern Pakistan, and thus, an interspecific situation resembling that of the mostly parapatric North American water snakes *Nerodia sipedon* and *Nerodia fasciata* (Mebert, 2008, 2010). In that relationship, *Nerodia sipedon* dominates the upland areas containing lotic systems (moving water bodies in hilly terrain and mountains inland), whereas *Nerodia fasciata* occupies the lentic system (slow moving or standing water bodies). The two *Nerodia* species build mixed populations and large hybrid zones, where there is a transition zone between their preferred and slightly distinct habitats. In Asia, it's *N. tessellata* that normally associates with lotic habitat, as also reflected by the two Pakistani sites near rivers and ample ecological information about this species (see refs. in Mebert, 2011a), whereas *X. piscator* normally is linked to lowland and lentic habitat, inhabiting irrigation channels, large ponds with dense emergent vegetation and tributaries (Minton, 1966; Karsen *et al.*, 1998; Khan, 2002; Teynié and David, 2010; Masroor, 2012).

However, the two water snakes from Pakistan

do not show such distinct habitat occupancy. A combination of unvouchered reports provided to us by Muhammad Sharif Khan (MSK), a foremost expert on the herpetofauna of Pakistan, and preserved specimens from the Khyber Pakhtunkhwa province confirm that it inhabits also hilly and mountainous areas as far north as (from west to east in Figure 2: Peshawar (UF 78948, see Fig. 1D), Malakand (Wall, 1923), Mardan, Mingora, Swabi approx. 20 km west of Tarbela Dam Lake (latter three sites by MSK, pers. comm.), Khanpur Dam Lake north of the Margalla Hills National Park (PMNH 371 and Masroor, 2012), the suburban of the nation's capital, Islamabad (PMNH 941 and 1895), and near Datta (southeast of Mansehra) at 1,250 m a.s.l. Two *X. piscator* records from sites 100 km farther south at around 660 m a.s.l. near Tata Pani and Goi Madan-Kotli (the two far right green dots in Fig. 2), both villages in Azad Jammu and Kashmir Federal Territory, are also within hilly country. But the most surprising find in this context is the observation of a *X. piscator* close to 2,000 m a.s.l. at Kalam in the far upper Swat Valley (MSK, pers. comm.) in an alpine landscape of fast flowing torrent water flanked by forested tall and steep mountains (the most northern green dot without an "X" in the upper center of Figure 2). Similar are other records by Khan (1999) and two putative *X. piscator* from the deeply cut northern Indus north of Dudishal (~1,225 m a.s.l.) and in the Tangir valley north of Sazin (~2,000 m a.s.l.) reported by wildlife personnel after presenting them photographs of respective species (Masroor, 2012 and two green dots in Figure 2 filled with an X to reflect the lack of species identification by an expert). Even though, *X. piscator* could be confused externally and ecologically with another snake occurring in northern Pakistan, the semi-aquatic and fish eating racer *Platyceps rhodorachis* (Egan, 2007), Whitaker's (2006) high elevation records of *X. piscator* up to 3,000 m a.s.l. in more eastern and warmer Himalaya (but see below) corroborate the plausibility of the checkered keelback inhabiting these western Karakoram valleys.

Although the northern limits of *X. piscator* in Pakistan are not precisely known, the records show that this species occurs well into hilly terrain with lotic aquatic systems of the southern versant of the Karakoram Mountain Range. On the other hand, *N. tessellata* may inhabit the lentic systems, such as ponds and marshes in northern Pakistan, habitats usually associated with *X. piscator* farther south, but for which *N. tessellata* is known in areas outside Pakistan (see refs. in Mebert, 2011a). For example, the new find of *N. tessellata* from the wetlands at Gahkuch is within a lentic system, which though is next to the Ghizer River, a lotic system. Hence, both water snake species likely would colonize any aquatic habitat that provides adequate prey supply, harbors abundant shelter for predator avoidance and hibernation, and provides a climate sufficient for relevant life history traits related to growth and reproduction. This raises the question, whether there is some area of contact between these water snakes and what nature would be their interaction.

Various studies in the recent past, involving *N. tessellata* and a second, ecologically similar *Natrix* species, show that partial coexistence among these natricines is possible in some cases (Janev Hutinec and Mebert, 2011; Scali, 2011), whereas in other cases, competition appears to be responsible for the decline of the *Natrix* species other than *N. tessellata* (Metzger *et al*., 2009, 2011; Mazza *et al*., 2011). However, an interspecific relationship may depend on a multitude of factors and the degree of their overlap, as well as the limit of resources consumed or required by both taxa to compete with each other. In our study area, both, *N. tessellata* and *X. piscator*, are feeding on semi- to fully-aquatic prey (fish and anurans) and occupy a broad niche of water habitats from lentic to lotic systems (Mebert, 2011a; Khan, 1999, 2002). Despite these similarities in habitat requirements, there is no explicit information that *N. tessellata* and *X. piscator* occur in sympatry at any site in Pakistan or elsewhere, let alone coexist in a competitive relationship with each other. Yet, some potentially overriding interspecific differences in ecological niches can be deduced from published data. Whereas *N. tessellata* is predominantly a water snakes of temperate zones and semi-arid steppes, enduring quite dry climates and cold winters (Kotenko *et al*., 2011; Litvinov *et al*., 2011; Liu *et al*., 2011), *X. piscator* is a tropical species, occurring in humid-warm areas from the Indus River system south of the Himalaya as far east as north-western Thailand (Vogel and David, 2007;

Teynié and David, 2010). This is consistent with temperature data at which both species are found. The two Pakistani sites of *N. tessellata* experience a annual mean temperature of 12–14°C (based on the years from 1971–2000), whereas *X. piscator* in Pakistan are all from sites with > 16 C° annual mean temperature (Climate Maps at CDPC, Pakistani Meteorological Department 2012). The rainfall map by the CDPC does not show any correlation with the ranges of either species. However, as already stated above, *N. tessellata* is known to have colonized similar low-elevated alluvial plains as those currently occupied by *X. piscator* in Pakistan. For example, lowland sites in the Basra wetlands, Iraq, where *N. tessellata* is abundant, yields an average annual mean temperatures of 24.4°C. Average annual mean temperatures are 22.0 C° for Cairo, Egypt, where *N. tessellata* inhabits the Nile and nearby irrigation systems. These mean temperatures are comparable to sites in Pakistan, that are exclusively occupied by *X. piscator* today, *e.g.*, Lahore 23.4°C (mean over 8 years, climate-zone.com), Peshawar 22.7°C and Islamabad 21.4°C (mean of 1951–2000, Ghaffar and Javid, 2011). It does show, that high temperatures are unlikely to prevent *N. tessellata* from expanding farther southward in Pakistan. In contrast for the checkered keelback, for which the cool and particular dry temperatures in the western Himalayan valleys could be a barrier to colonization or moving northward. Although Whitaker (2006) gives a generic altitudinal range of *X. piscator* up to 3,000 a.s.l. in the Himalaya, he provided no concrete examples or precise locations. We presume, in accordance with the title of his paper, that this account refers to Indian checkered keelbacks from the more humid and warmer central to eastern Himalaya compared to the western Himalaya (Chatterjee and Bishop, 2012). At least, we are not aware of *X. piscator* inhabiting such cool sites in the Karakoram Mountain Range of the western Himalaya as those experienced by *N. tessellata* in northern Pakistan, and thus, this indicates an important ecological difference between these two semi-aquatic snakes.

Nonetheless, a contact zone may exist, where interspecifically distinct ecological features are transitional. Are there such areas in northern Pakistan that constitute an environmental transition zone, where both taxa can occur in sympatry. Unfortunately, a large area of up to 50,000 km^2 in northwestern Pakistan, next to the currently known range limits of and between both water snake species, exhibit plenty of suitable habitats but lack any vouchered species identification to this day. Hence, the exact localization of a potential contact zone is impossible at this point. However, a partial approach to the missing contact zone can be achieved. Pictures of two preserved *X. piscator* from around Jalalabad, Afghanistan, near the border with Pakistan, were provided to us. They currently represent the only known specimens of this species from Afghanistan. A first specimen is labelled as *X. piscator* (CAS 120542, see Fig. 1F) and originates from 40 km southwest of Jalalabad (farthest left green dot in Fig. 2), Nangarhar Province, Afghanistan, at 3450 ft. (~ 1,050 m a.s.l.). Expression of pholidotic characters and color pattern show that this specimen agrees in all aspects with *X. piscator*, and not with *N. tessellata*. The distance to Jalalabad and altitude indicated on the label place that specimen to a tributary of the Darya ye-Sang Lech River, west of the village Amankhel. The river bed consists of a cultivated alluvial plain flanked by gently rising hills with semi-arid slopes and some mountains rising to > 1,500 m a.s.l. A second water snake from that region (Jalalabad, ZFMK-H 8652, Fig. 1G) is labelled as *X.* "*sanctijohannis*" (= *X. piscator* acc. Vogel and David, 2012). The relevance of these two specimens is, that they were found (a) in a habitat typical for *N. tessellata* from central Asia, (b) are from tributaries to the Kabul River, which itself supports populations of *N. tessellata* east of Kabul (Paghman: CAS 115972, FMNH 161179/80; Jalriz: ZFMK 14542/43/44) at about 150–200 km upstream from these "*X. piscator*-sites", and (c) are in proximity to the confluence of the Kabul River and Kunar River east of Jalalabad, which itself connects approximately 320 km upstream to Mastuj in Pakistan from where the first Pakistani finds of *N. tessellata* by Wall (1911) originate. These points are indications that the two water snake species either could exist in sympatry around Jalalabad, or *X. piscator* may have replaced *N. tessellata* there, with populations of latter species surviving only at sites

more upstream. The very narrow Mahipa Gorge along the Kabul River west of Jalalabad may constitute an ecological barrier for both water snakes to exchange. But no such narrowing habitat is known from the Kunar River upstream (upper leg of Route 3 on Fig. 2), opening a potential colonization route up to the *N. tessellata* at Mastuj. Hence, only further prospecting this area will reveal, whether Jalalabad and rivers upstream represent a zone of sympatry of *N. tessellata* and *X. piscator*, and thus enabling potential competitive interactions between these water snakes taxa. Moreover, the area along Route 3 would have also been used by *N. tessellata* to reach the newly discovered site a Gahkuch, if they were not to surmount high passes (> 3,000 m a.s.l.) due to unsuitable climate. This Route 3 from Mastuj would lead over > 1,000 km along the linked river systems Chitral-Kunar-Kabul Indus up into the Ghizer Valley Gilgit-Baltistan. Following this route, *N. tessellata* would have passed through areas inhabited by *X. piscator* in Pakistan today. However, as *N. tessellata* is not known from sites along this route occupied by *X. piscator*, and as there should have been sufficient time to expand via this route (Route 3) since the start of the postglacial expansion (see first scenario above), we infer that competitive exclusion is or has been at work here.

Concluding from the locality information on both water snake species in northern Pakistan herein analyzed, we tentatively presume that this represents the current interspecific situation in northern Pakistan. *X. piscator* ventures far into lotic systems in valleys of the southern versant of the western Himalaya, a habitat rather associated with *N. tessellata* elsewhere (Mebert, 2011a), but its progression is halted by climatic factors, such as low temperatures and possibly humidity or amount of rainfall. Expansion southward by *N. tessellata* is prevented by competitive exclusion through *X. piscator*, which is the more successful species in the south-draining valleys of the western Himalaya and the lentic systems of the Indus River farther south. But it required the analysis of all four scenarios to come to this conclusion. Unfortunately, current and long lasting political instability stretches over most areas, where the contact zones between *N. tessellata* and *X. piscator* likely is situated. Hence, this paper can only reflect on the current status of knowledge of *N. tessellata* in Pakistan and Afghanistan, and simultaneously motivate future studies as soon as the situation on the ground allows it.

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