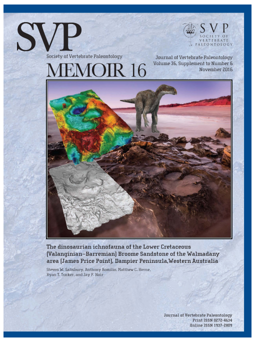

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ARTICLE

NEW EARLY LATE MIOCENE SPECIES OF *VISHNUONYX* (CARNIVORA, LUTRINAE) FROM THE HOMINID LOCALITY OF HAMMERSCHMIEDE, BAVARIA, GERMANY

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ABSTRACT—This study presents a new species of a large-sized lutrine from the upper Miocene hominid locality of Hammerschmiede, *Vishnuonyx neptuni* sp. nov., reporting the first occurrence of the genus in Europe and its most northern and western record. The new species differs from the already known members of the genus in size (intermediate between the African *Vishnuonyx*? *angololensis* and the Asiatic *Vishnuonyx chinjiensis*) and morphology, in particular in the larger P4 hypocone, the primitive morphology of M1 (paraconule present, enlarged protoconule and metaconule, labial expansion at the paracone area), the shorter and more robust lower premolars and the wider m1 trigonid. We hypothesized that the dispersal event that led to the expansion of the genus in Europe seems to be correlated with the water connection between Paratethys and the Mesopotamian Basin during the Konkian, between 13.4 and 12.65 Ma. In terms of paleoecology, it is here suggested that this form was feeding mainly on fish and less on bivalves or plant material, resembling the extant giant otter, *Pteronura brasiliensis*.

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INTRODUCTION

Hammerschmiede

The locality of Hammerschmiede has been studied for nearly half a century (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975). At least six distinct fossiliferous levels have been identified, but the majority of fossils has been unearthed from the fluvial channels HAM 4 and HAM 5, dated to 11.44 and 11.62 Ma, respectively (Kirscher et al., 2016). Several studies have been published concerning the fauna (both vertebrate and invertebrate) of the locality (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975; Schneider and Prieto, 2011; Fuss et al., 2015; Böhme et al., 2019, Mayr et al., 2020a, 2020b; Hartung et al., 2020; Kargopoulos et al., in press). They reveal an extremely high faunal diversity, comprising more than 130 terrestrial and aquatic vertebrate species, several being new to science. The hominid *Danuvius guggenmosi* Böhme et al., 2019, from Hammerschmiede, has been suggested to involve a degree of bipedalism in its locomotion (Böhme et al., 2019, 2020). So far, the only study solely concerning the carnivorans from Hammerschmiede is that of Kargopoulos et al. (in press), reporting the presence of the viverrids *Semigenetta sansaniensis* (Lartet, 1851) and *Semigenetta grandis* Crusafont-Pairó and Golpe Posse, 1981. Here we present the first remains of a bunodont otter from the locality.

Bunodont Otters

The subfamily Lutrinae includes the extant otters sensu lato and their fossil relatives. The phylogeny and systematics of the subfamily above the genus level are far from resolved (e.g., Willemsen, 1992; Bryant et al., 1993; Morales and Pickford, 2005a; Fulton and Strobeck, 2006; Pickford, 2007; Koepfli et al., 2008; Agnarsson et al., 2010; Wang et al., 2018; Hassanin et al., 2021). The clustering scheme becomes even more obscure with the consideration of Potamotheriinae (Pickford, 2007; Rybczynski et al., 2009; Paterson et al., 2020) and the group of *Lartetictis* Ginsburg and Morales, 1996, *Mionictis* Matthew, 1924 and *Siamogale* Ginsburg, Ingavat and Tassy, 1983 (Ginsburg, 1999; Wang et al., 2018; Valenciano et al., 2020).

Bunodont otters are a paraphyletic group of large- to very large-sized otters from North America, Eurasia, and Africa. It includes the genera *Djourabus* Peigné, de Bonis, Likius, Mackaye, Vignaud and Brunet, 2008; *Enhydriodon* Falconer, 1868; *Enhydritherium* Berta and Morgan, 1985; *Paludolutra* Hürzeler and Engesser, 1976; *Sivaonyx* Pilgrim, 1931; *Torolutra* Petter, Pickford and Howell, 1991; and *Vishnuonyx* Pilgrim, 1932 (Morales and Pickford, 2005a; Pickford, 2007; Grohé et al., 2020). Additionally, the genera *Enhydra* Fleming, 1822, *Aonyx* Lesson, 1827, and *Enhydrictis* Forsyth Major, 1901, have been considered to be close to these forms (Morales and Pickford, 2005a; Pickford, 2007; Valenciano and Govender, 2020). However, recent studies

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have removed *Enhydrictis* from the Lutrinae, considering it as a member of the Ictonychinae (Galictini sensu Rook et al., 2018, or Lyncodontini sensu Jiangzuo et al., 2019). The bunodont otters are characterized by a robust dentition, with strong cingula and tall and dull cusps. The developed lingual cusps in P4 (hypocone and protocone) are positioned considerably lingually to the carnassial blade, establishing a large valley between them. Additionally, they have a large distal accessory cuspid in the p4 and a deep mandibular corpus (Pickford, 2007 and references therein). Among them, the genera *Vishnuonyx* and *Torolutra* possess the lesser bunodont appearance on their cusps. Moreover, an array of different lifestyles has been suggested for these forms, ranging from terrestrial to semi-aquatic (Lewis, 2008; Peigné et al., 2008; Geraads et al., 2011; Werdelin and Lewis, 2017; Valenciano and Govender, 2020). The robustness of the mandibles and the enhancement of crushing cheek teeth in *Djourabus*, *Enhydriodon*, *Enhydritherium* and *Sivaonyx*, have been associated with a diet based on mollusks and crustaceans (Pickford, 2007; Lewis, 2008), whereas Geraads et al. (2011) suggested that the large *Enhydriodon dikikae* Geraads, Alemseged, Bobe and Reed, 2011, was possibly able to consume even armored prey such as turtles, juvenile crocodiles, or ostrich eggs.

The genus *Vishnuonyx* (Fig. 1) was introduced by Pilgrim (1932) with *Vishnuonyx chinjiensis* Pilgrim, 1932 as the type species, based on material from the upper part of the Chinji stage in the Lower Siwaliks. Pilgrim (1932) described a maxilla with P4 and the root of the M1, and a hemimandible with a complete p4 and fragmentary m1 and m2. The exact age of the fossiliferous layer is unknown, but it was estimated to be of late middle Miocene or early late Miocene age (Nanda and Sehgal, 2005). This species has also been found in the Locality 2/11 in Ngorora D in Kenya (Morales and Pickford, 2005b; late middle Miocene; firstly reported in the faunal list of Ngorora Formation by Hill et al., 1985 as *Vishnuonyx* sp. nov.), in Ramnagar in India (Nanda and Sehgal, 1993, 2005; Sehgal, 2013; only as a member of the faunal list without describing any specimens; late middle Miocene) and in the loc. Y53 and loc. Y828 of the Potwar Plateau in Pakistan (Grohé et al., 2020; late middle Miocene). Therefore, the temporal range of *V. chinjiensis* is restricted to the late middle Miocene, with a possible expansion towards the early late Miocene, if the specimens of Pilgrim (1932) proved to be slightly younger. Additionally, Werdelin (2003) described a second species, *Vishnuonyx angololensis* Werdelin, 2003, based on an upper carnassial from Lower Nawata in Lothagam (late late Miocene). This species was later attributed to the genus *Torolutra* (Haile-Selassie, 2008; Werdelin and Lewis, 2017), but its generic status still remains doubtful (Grohé et al., 2020). Recently, Grohé et al. (2020) described the third identified species of the genus, *Vishnuonyx maemohensis* Grohé, de Bonis, Chaimanee, Chavasseau, Rugbumrung, Yamee, Suraprasit, Gibert, Surault, Blondel and Jaeger, 2020, from the middle–late middle Miocene of Mae Moh in Thailand. Furthermore, Haile-Selassie (2008) published a mandibular corpus with a lower carnassial from the Haradaso Member of the Middle Awash (early Pliocene) in Ethiopia as *Vishnuonyx* sp., which represents the last known occurrence of the genus in the fossil record. No postcranial material of *Vishnuonyx* has ever been found and a plesiomorphic semiaquatic lifestyle seems highly possible, due to the dental adaptations correlated to piscivory, as discussed below.

Therefore, no solid results regarding the taxonomy, evolution, biostratigraphy and paleoecology of bunodont otters (including the genus *Vishnuonyx*) have been reached to date. Additionally, details on the dispersal event of *Vishnuonyx* from South Asia towards the other regions of the Old World still are unclear. Consequently, every report that provides new knowledge on the fossil record of the group is decisive in order to solidify existing hypotheses on the aforementioned problems.

The present study deals with new craniodental material of a new species of *Vishnuonyx* from the upper Miocene locality of Hammerschmiede. The unexpected occurrence of the genus in Europe is investigated in terms of stratigraphy and paleogeography. Finally, an ecomorphological approach is employed in order to trace the diet specialization of the new species.

MATERIAL AND METHODS

The specimens studied herein come from the fluvial channel HAM 4 (11.44 Ma) of the fossil locality of Hammerschmiede (Bavaria, Germany) and they were unearthed during the excavations held by the Eberhard Karls University of Tübingen between 2011 and 2020. The material is stored in the Paleontological Collection of the University of Tübingen, Germany (GPIT) and is inventoried with numbers of both GPIT (for excavations from 2011 to 2019) and SNSB-BSPG (Bavarian State Collection of Paleontology and Geology in Munich, Germany; for excavations of 2020). The specimens coded as SNSB-BSPG 2020 XCIV were excavated from HAM 4 locality in 2020. Their codes in the tables are mentioned as BSPG 2020 XCIV for practical reasons.

Dental nomenclature follows Ginsburg (1999) and Smith and Dodson (2003). All measurements were taken with a digital caliper and rounded to the first decimal point. In cases of multiple specimens per skeletal element, the descriptions and comparison concern the material as a whole. The specimens were scanned in a Nikon XT H 320 μCT scanner using the 225 reflection target and the 'Helical CT Scan' function. The isolated teeth were scanned separately from the mandibles. The isolated teeth were scanned at 200 kV and 80 μA with a voxel size of 0.01847402 mm and 5864 projections, using a copper filter of 1 mm thickness. The mandibles were scanned at 185 kV and 86 μA with a voxel size of 0.01603859 mm and 6321 projections, using a copper filter of 1 mm thickness.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family MUSTELIDAE Fischer, 1817
Subfamily LUTRINAE Bonaparte, 1838
Genus *VISHNUONYX* Pilgrim, 1932

Diagnosis—Lutrinae of medium size; P4 triangular, labial mesiodistal length greater than lingual, and also much exceeding transverse diameter, parastyle weak, high pointed paracone, metastyle lower but elongated, protocone and hypocone much lower than paracone, protocone situated rather far forward; internal cingulum slight; M1 rather small, lingual platform reduced mesiodistally; mandible with deep ramus; p4 elongate with a distal widening and a broad cingulum, mesially tall, a high and strong distal accessory cuspid, more fused mesially with the main cuspid than in *Sivaonyx*; m1 with talonid shorter than trigonid, surrounded by a crenulated rim; m2 oval, rather longer than in *Sivaonyx*. [Modified after Werdelin and Peigné (2010) and Grohé et al. (2020).]

Type Species—*Vishnuonyx chinjiensis* Pilgrim, 1932.

Other Included Species—*V.*? *angololensis* Werdelin, 2003, *V. maemohensis*, *V. neptuni* sp. nov.

VISHNUONYX NEPTUNI sp. nov.
(Figures 2 & 3, Tables 1 & 2)

Holotype— a right hemimandible, SNSB-BSPG 2020 XCIV-0301, with p1 alveolus and complete p2–m1 from HAM 4.

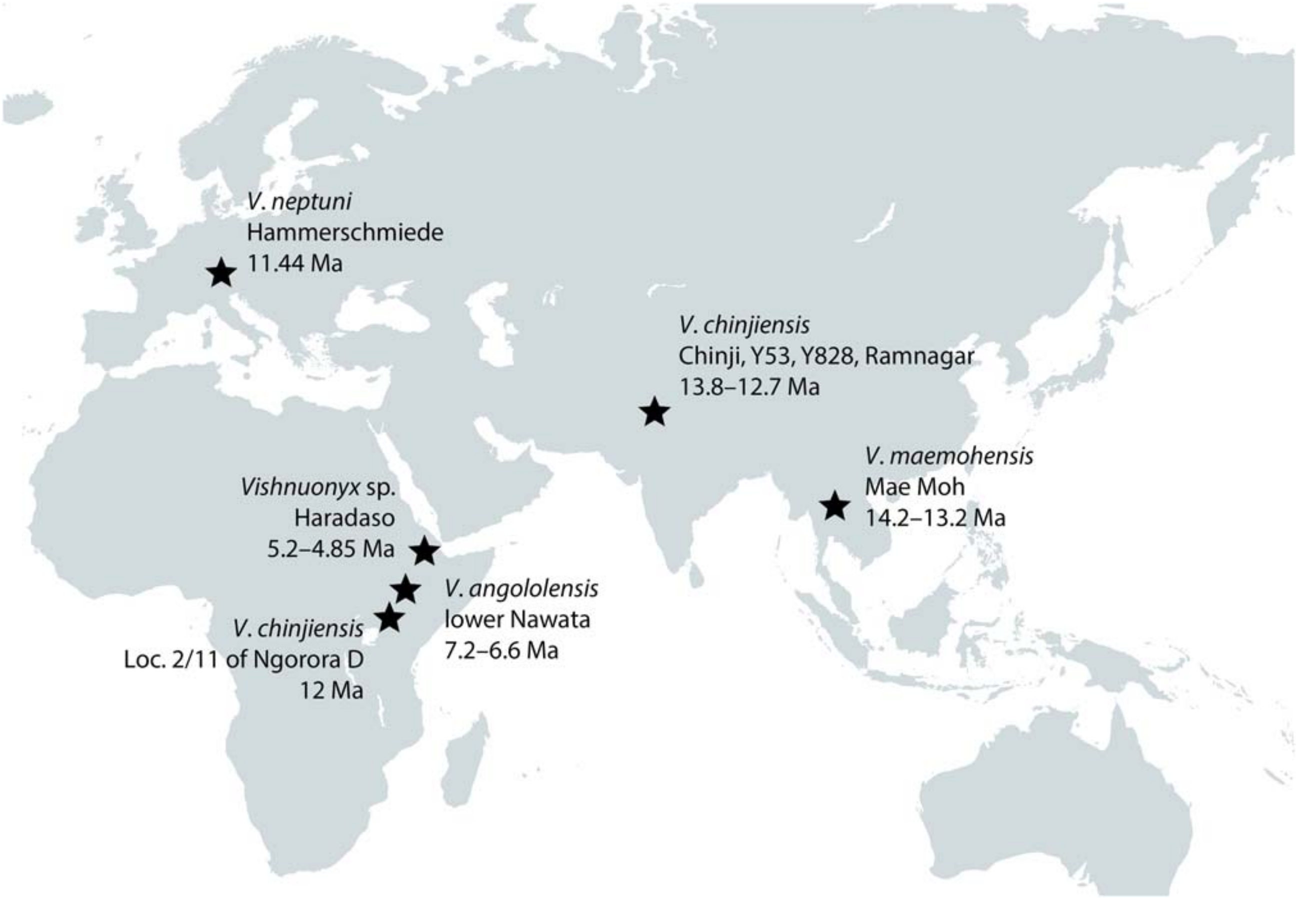

FIGURE 1. Temporospatial distribution of the known species of the genus *Vishnuonyx*.

Hypodigm— SNSB-BSPG 2020 XCIV-1022, left P3; GPIT/MA/17347, right P4; SNSB-BSPG 2020 XCIV-1552, left M1; GPIT/MA/16733, left hemimandible with p3–m1; SNSB-BSPG 2020 XCIV-1301, right p4.

Etymology—The name *neptuni* is derived from Neptune, the Roman god of water.

Type Locality—HAM 4, Hammerschmiede, Bavaria, Germany (11.44 Ma) (Fig. 1).

Diagnosis—Species of *Vishnuonyx*, intermediate in size between the larger *Vishnuonyx*? *angololensis* and the smaller *Vishnuonyx chinjiensis* and *Vishnuonyx maemohensis*; p2 bent labially; P4 hypocone large, similar in size with the protocone; M1 paraconule present and small; M1 protoconule and metaconule present and large; M1 expansion labially to the paracone enhanced; lower premolars relatively short; m1 trigonid slightly wider than m1 talonid.

Differential Diagnosis—Differs from Lutrini in the enlarged P4 hypocone, the mesiodistally narrower M1, the larger distal accessory cuspid of p4, the shorter m1 talonid, the higher m1 trigonid cuspids and a higher m1 protoconid. Differs from Aonychini in the larger P4 hypocone, the narrower M1, the more enlarged p4 distal accessory cuspid, the narrow m1 talonid and the higher m1 trigonid cuspids. Differs from the group of *Siamogale*, *Mionictis*, and *Larteticti*s in the more developed protocone area of P4, the narrower M1, the labial position of the distal accessory cuspid in p4 and the higher m1 trigonid cusps. Differs from the Potamotheriinae in the absence of a carnassial notch in P4, the presence of a hypocone, the presence of M1 paraconule and metaconule, the absence of mesial accessory cuspids in p3 and p4 and the blunter m1 trigonid. Differs from the derived bunodont otters (tribe Enhydrini sensu Pickford, 2007; *Enhydra* and *Enhydritherium*), as well as from *Enhydriodon* and *Paludolutra* in the absence of wide occlusal surfaces and bunodont cusps. Differs from *Sivaonyx* by the (usually) smaller size, the less developed protocone region of P4, the less developed m1 talonid, the smaller m1 metaconid and the smaller m2. Differs from *Torolutra* in the larger P4 hypocone, the absence of P4 protoconule, the less developed p4 distal accessory cuspid and the more robust m1 trigonid.

Differs from *V. chinjiensis* in the larger size, the shorter premolars, the more robust P4 with a more developed hypocone and stronger cingulum and parastyle, the higher m1 metaconid and the relatively slenderer talonid. Differs from *V. maemohensis* in the larger size, the shorter premolars, the more robust P4 with a stronger cingulum and parastyle, the presence of M1 paraconule, the larger M1 protoconule and metaconule, the less reduced M1 lingual platform, the less convex outline of the lower teeth, the sharper p3 and the presence of a mental foramen below p2. Differs from *V.*? *angololensis* in the smaller size, the presence of P4 parastyle, the larger P4 hypocone, the more distally situated P4 protocone and the more robust P4 cingulum.

Description—The P3 (SNSB-BSPG 2020 XCIV-1022; Fig. 2A) is asymmetrical with the distal side being larger than the mesial one. A mesial, a distal and a lingual crista diverge from the main cusp. It has three roots. The lingual ridge ends up in an expansion of the lingual wall of the tooth that also hosts an additional root. The cingulum is relatively robust and the enamel wrinkled.

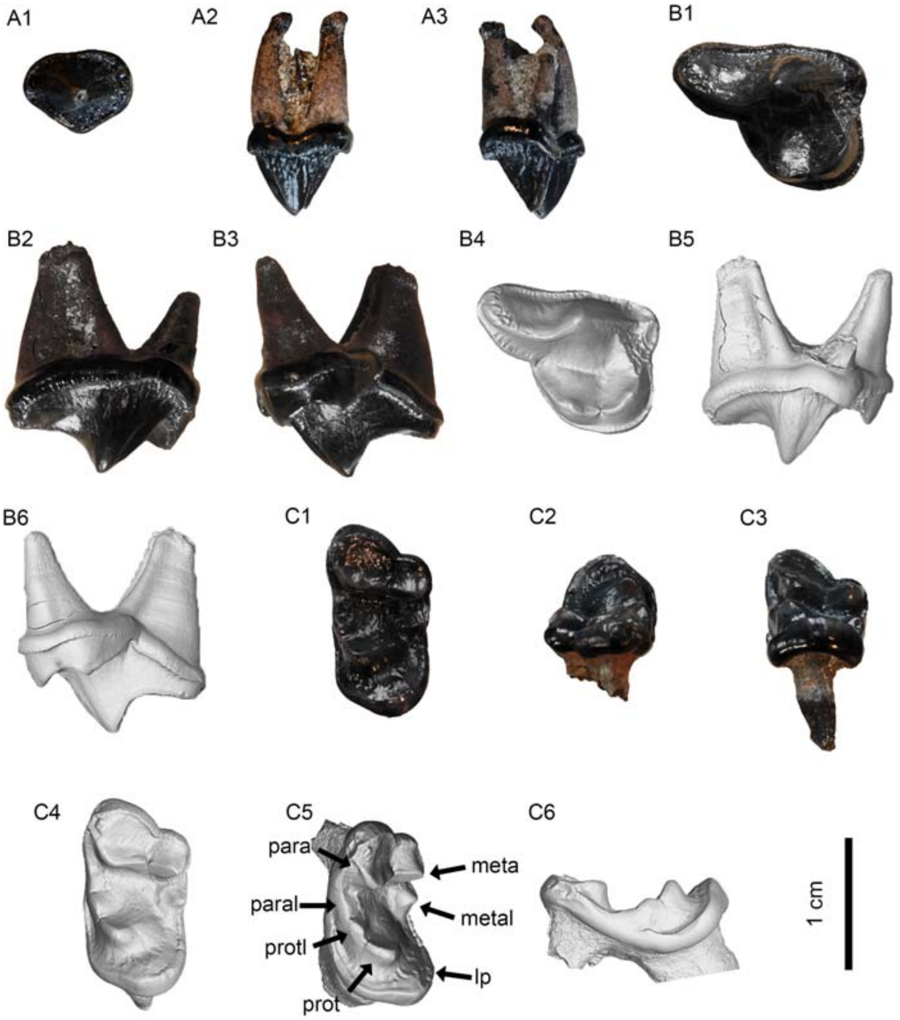

FIGURE 2. The upper dentition of *Vishnuonyx neptuni* sp. nov. **A**, SNSB-BSPG 2020 XCIV-1022, left P3 in occlusal (A1), labial (A2) and lingual (A3) views; **B**, GPIT/MA/17347, right P4 (original specimen and screenshots of its 3D model) in occlusal (B1, B4), labial (B2, B5) and lingual (B3, B6) views; **C**, SNSB-BSPG 2020 XCIV-1552, left M1 (original specimen and screenshots of its 3D model) in occlusal (C1, C4), labial (C2), lingual (C3), mesial-occlusal (C5) and mesial (C6) views. **Abbreviations**: **meta**, metacone; **metal**, metaconule; **lp**, lingual platform; **para**, paracone; **paral**, paraconule; **prot**, protocone; **protl**, protoconule.

The available upper carnassial (GPIT/MA/17347; Fig. 2B) is complete, with a moderately developed wear facet on its carnassial blade and a strong cingulum through the whole perimeter of the tooth. The paracone is high and acute, forming a fine crest with the metastyle, without a carnassial notch. It has a small parastyle at the mesial cingulum. A large valley-shaped shelf is present between the labial and lingual cusps. The protocone is wide and high, standing mesially to a hypocone of similar size and morphology. The two lingual cusps are connected by two small crests that merge in an indistinct notch. The protocone is situated between the planes of the paracone and the parastyle, while the hypocone is situated slightly distally to the plane of the paracone. In terms of height, paracone is the highest cusp, followed by the metastyle, the lingual cusps, and lastly the parastyle.

TABLE 1. Comparison of the upper teeth dimensions of *Vishnuonyx neptuni* sp. nov. with other species of *Vishnuonyx*. The parentheses indicate measurement taken at the alveolus. Data from: Grohé et al. (2020).

Species	Code	P3L	P3W	P4L	P4W	M1L	M1W
Vishnuonyx neptuni sp. nov.	BSPG 2020 XCIV-1022	7.8	6.0				
	GPIT/MA/17347			13.4	10.4		
	GPIT/MA/10505					(7.9)	13.3
	BSPG 2020 XCIV-1552					7.6	14.0
Vishnuonyx chinjiensis	GSI D 223			11.5	9.1		
	GSP-Y 2108			10.2	7.8		
	KNM-BN 1730			11.6	9.4		
Vishnuonyx maemohensis	MM-36			12.2	8.6		
	MM-37					5.3	11.1
	MM-78 left	6.5	4.5	11.9	8.3	5.9	11.5
	MM-78 right	6.7	4.6	11.7	8.4	5.0	
Vishnuonyx? *angololensis*	KNM-LT 23948			15.3	12.9		

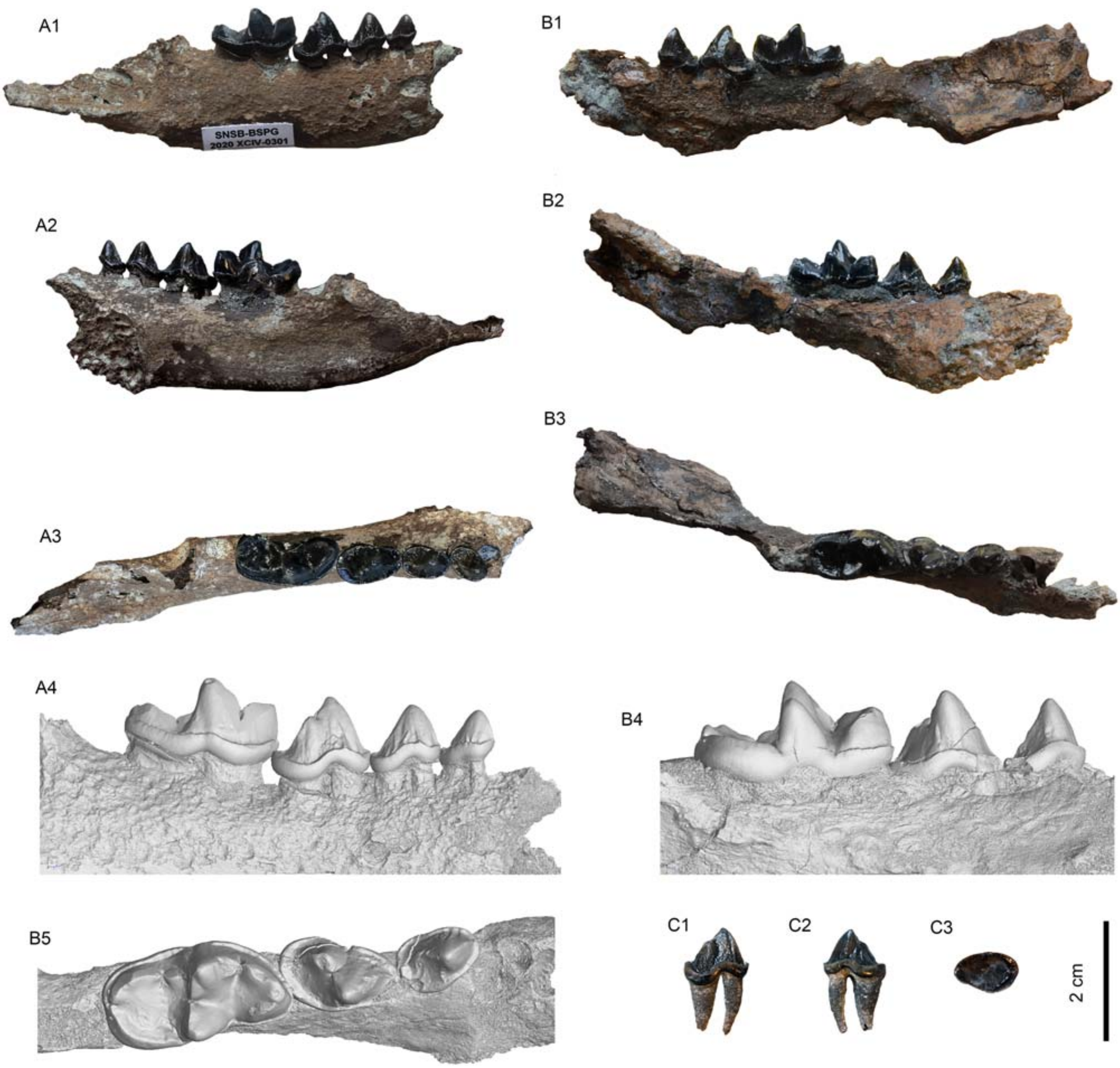

FIGURE 3. The lower dentition of *Vishnuonyx neptuni* sp. nov. **A**, SNSB-BSPG 2020 XCIV-0301, right hemimandible (holotype; original specimen and screenshots of its 3D model) in labial (**A1**, **A4**), lingual (**A2**) and occlusal (**A3**) views; **B**, GPIT/MA/16733, left hemimandible in labial (**B1**), lingual (**B2**, **B4**) and occlusal (**B3**, **B5**) views; **C**, SNSB-BSPG 2020 XCIV-1301 right p4 in labial (**C1**), lingual (**C2**) and occlusal (**C3**) views. Screenshots of the 3D models not in scale.

The upper molar (SNSB-BSPG 2020 XCIV-1552; Fig. 2C) is complete and slightly worn at the lingual side of the paracone and the metacone. A developed cingulum is present in the perimeter of the tooth, being less developed in its mesial part. The outline of the tooth is slender and almost rectangular. The labial border of the tooth is more enhanced at the paracone level than in the metacone level. The paracone and the metacone are approximately of equal height, but the paracone is considerably wider. They are connected with a low crest that forms a small notch in its center. Lingually to these two cusps there is a shallow valley, where a metaconule and a well-developed protoconule (bordered by two clear notches) are located. A postmetaconular crista is present, as well as a postprotocrista (almost reaching the metaconule) and a preparaconular crista reaching the mesial cingulum and hosting a small crest-like paraconule. The lingual platform is mesiodistally short, in relation to the extant lutrines.

None of the two preserved hemimandibles is complete. SNSB-BSPG 2020 XCIV-0301 preserves part of the alveolus of the canine, part of the angular process and part of the masseteric fossa (Fig. 3A). The masseteric fossa is deep cranially and shallow caudally. The caudal part of the mandible is bent labially, while the angular process is small and hook-like. The hemimandible GPIT/MA/16733 is heavily damaged (Fig. 3B), so only the cheek teeth, part of the canine alveolus and part of the masseteric fossa are preserved. Over the ventral part of the masseteric fossa, it exhibits a large area for the insertion of M. masseter pars superficialis and M. pars profunda. The mandibular ramus of SNSB-

TABLE 2. Comparison of the lower teeth dimensions of *Vishnuonyx neptuni* sp. nov. with other species of *Vishnuonyx*. The parentheses indicate measurements taken at the alveolus. Data from Grohé et al. (2020).

Species	Code	p1L	p1W	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1Ltr	m1W	m2L	m2W
Vishnuonyx neptuni sp. nov.	GPIT/MA/16733					6.6	4.8	8.9	6.2	14.6	10.4	7.7		
	BSPG 2020 XCIV-0301	(4.0)	(3.3)	5.7	4.1	6.6	4.6	9.0	5.7	14.1	9.6	(7.3)	(3.5)	(3.2)
	BSPG 2020 XCIV-1301							9.9	6.5					
Vishnuonyx chinjiensis	GSI D 245							7.3	4.2	11.7			5.0	3.3
	WIHG FR 24/18							7.2	4.3					
	GSP-Y 40764									12.2	7.5	5.9		
Vishnuonyx maemohensis	MM-30 left					6.2	3.7	8.3		11.8	7.8	6.2	4.5	4.2
	MM-30 right	3.5	2.6	5.3	3.1	6.1	3.7	8.2	4.6	11.9	7.8	6.0	4.5	4.2
	MM-32									12.1	7.8	6.4		
	MM-33							7.6	4.1	10.6	6.7	5.8		
	MM-34			5.1	2.9	5.3	3.1	6.7	3.5	10.5	7.1	5.2		
	MM-35					5.2	3.4	7.7		11.1	7.3	5.8		
	MM-79							7.1	3.5	10.7		4.8	3.4	2.3
Vishnuonyx sp.	GAW-VP-1/1									13.5	8.2	7.2		

BSPG 2020 XCIV-0301 is moderately robust and it has one large mental foramen, below the p2. The mandibular symphysis is inclined cranially.

The canine is absent, but its alveolus is enlarged in both hemimandibles. One small alveolus for the p1 is also present and in proximity to the p2. The p2 is two-rooted, unicuspid and asymmetrical, with a well-developed cingulum, especially in its labial and distal part. The long axis of the tooth is not aligned with the long axis of the whole toothrow. Both p3 and p4 are high and pointed premolars, with their main cuspids being mesially located and distally inclined. The p3 is relatively high, unicuspid with a rough labial surface with many small wrinkles. The p4 is much larger than p3 and higher than the m1 paraconid. It also possesses a developed cingulum (mesially crowned) and a large distal accessory cuspid, situated at the distolabial ridge of the main cuspid. The m1 is significantly broad, with the talonid covering almost one third of the length of the tooth. The trigonid is slightly wider than the talonid. A strong cingulum surrounds the entire tooth. The trigonid exhibits small wear facets on the carnassial blade in GPIT/MA/16733, whereas in SNSB-BSPG 2020 XCIV-0301 the wear is more evident. The protoconid is the highest cusp. It is separated by the much smaller paraconid by a shallow notch. The metaconid is very developed. It is robust, slightly inclined lingually and it has approximately the same height as the paraconid. The talonid valley is large and deep. Two small labial cuspids (hypoconid and hypoconulid) are present on the talonid. They have approximately the same height, the hypoconid is continued mesially by a relatively long crest and the hypoconulid is labiodistally situated. A small cuspid (protoconulid/mesoconid) is located between the protoconid and the hypoconid. The distal cristid of the protoconid (also called mesoconid in literature) and the mesial cristid of the hypoconid form a carnassiform notch between them. The entoconid is absent. The lingual wall of the talonid is V-shaped. The alveolus for m2 is heavily damaged, but it is evident that it is of a relatively moderate size and a nearly circular outline.

DISCUSSION

Comparison

The material exhibits considerable differences with the typical morphology of the Lutrini sensu Willemsen (1992). The developed P4 hypocone, the mesiodistally slender M1, the more developed distal accessory cuspid of p4, the relatively short m1 talonid, the high m1 trigonid cuspids and especially the protruding m1 protoconid are traits that differentiate the Hammerschmiede material from the Lutrini (van Zyll de Jong, 1987; Willemsen, 1992; Pickford, 2007; Peigné et al., 2008).

Regarding the differences of the studied specimens from the tribe Aonychini (sensu Willemsen 1992, comprising the genera *Aonyx*, *Amblonyx* Rafinesque, 1832, *Cyrnaonyx* Helbing, 1935, *Limnonyx* Crusafont Pairó 1950, and *Megalenhydris* Willemsen and Maletesta, 1987), the members of this group have a wide M1, P4 hypocone reduced or absent, p4 with reduced or absent accessory cusp, and a very wide m1 talonid and m1 trigonid with low cuspids in relation to the Hammerschmiede specimens (van Zyll de Jong, 1987; Willemsen, 1992; Pickford, 2007; Peigné et al., 2008).

The genera *Siamogale*, *Mionictis*, and *Larteticitis* form a diverse group of otter-like mustelids from the middle to late Miocene, found in several localities of Eurasia and North America (e.g., Matthew and Gidley, 1904; Matthew, 1924; Ginsburg and Morales, 1996; Peigné, 2012; Wang et al., 2018; Grohé et al., 2020; Valenciano et al., 2020). They represent a group with uncertain affinities both among them and with other mustelid groups, being colloquially named as badger-like otters, because of their robust and bunodont dentition (Wang et al., 2018). *Vishnuonyx neptuni* sp. nov. undoubtedly differs from these species in the more developed protocone area of P4, the mesiodistally slenderer M1, the more labially situated distal accessory cuspid in p4 and the higher m1 trigonid cusps. These differences are more evident particularly with *Siamogale* spp. and *Larteticitis* spp.

The group of *Potamotherium* is also compared here because of its morphological affinities with the lutrines, regardless of its exact phylogenetic position. This genus has been reported with two species, the smaller *Potamotherium valletoni* Geoffroy, 1833 from the upper Oligocene and the lower Miocene (Savage, 1956; Mödden and Wolsan, 1993; Mörs and von Koenigswald, 2000) and the larger *Potamotherium miocenicum* (Peters, 1869) from the early middle Miocene, both from France and Germany (Thenius, 1949; Fahlbusch, 1967; Ginsburg, 1968). This genus has a very primitive dentition, and therefore several traits distinguish it from the otter from Hammerschmiede. Among them are a P4 with a carnassial notch, a distinct angle between the two parts of the carnassial blade, the absence of the P4 hypocone, the absence of paraconule, protoconule and metaconule in M1, the much more developed M1 parastyle, the more acute M1 lingual platform, the lower premolars are shorter, having a more bunodont aspect, both p3 and p4 have mesial and distal accessory cuspids with the distal one being more detached from the main cuspid and the m1 talonid is sharper (Thenius, 1949; Savage, 1956; Fahlbusch, 1967; Ginsburg, 1968; Mörs and von Koenigswald, 2000).

Compared with the Enhydrini, the post-canine dentition of *V. neptuni* sp. nov. is far slenderer with no distinct crushing surfaces (sensu Pickford, 2007, containing the genera *Enhydra* and *Enhydritherium*). The genus *Enhydriodon* also has far more developed occlusal surfaces and bunodont cusps in each cheek tooth (Pickford, 2007 and references therein). A similar morphology of the cheek teeth is also evident in *Paludolutra* (Hürzeler, 1987; Pickford, 2007).

The genus *Sivaonyx* is known from several species from Africa and Eurasia. The first record of *Sivaonyx* was made by Lydekker (1884), who identified the species *Sivaonyx bathygnathus* (as *Lutra bathygnathus*) from the Late Miocene of Punjab (India). The only representative of the genus in Europe is *Sivaonyx hessicus* from Eppelsheim firstly described by Lydekker (1890) as *Lutra hessica*. The genera *Vishnuonyx* and *Sivaonyx* have been proposed to have close affinities (Pickford, 2007). The specimens from Hammerschmiede differ from this genus by the less developed lingual shelf of P4, the far more restricted m1 talonid (both in length and in width), the lesser development of the m1 entoconid-cristid, the smaller m1 metaconid and the smaller m2, while most *Sivaonyx* species are far larger than *Vishnuonyx* (Pilgrim, 1931, 1932; Pickford, 2007; Grohé et al., 2013).

The African genus *Torolutra* from the early Pliocene is scarcely known and shares several traits with *Vishnuonyx*, making the distinction between the two genera intricate (Werdelin and Lewis, 2007; Haile-Selassie, 2008; Grohé et al., 2020). However, it differs from the Hammerschmiede material in the following traits: P4 hypocone smaller than the protocone, P4 protoconule present, p4 distal accessory cuspid less robust and more robust m1 trigonid (Petter et al., 1991; Morales et al., 2005; Haile-Selassie, 2008; Grohé et al., 2020).

The morphological features of the described specimens from Hammerschmiede fit perfectly with the diagnostic characters of the genus *Vishnuonyx*. The moderately developed protocone region of P4, the presence of a P4 hypocone of comparable size with the P4 protocone, the mesiodistally slender M1 with a reduced lingual platform, the strong and labially situated distal accessory cuspid in p4, the high m1 protoconid and the short m1 talonid suffice for the attribution of the Hammerschmiede material to this genus.

Metrically, the type species *V. chinjiensis* is significantly smaller than *V. neptuni* sp. nov. (Tables 1 and 2). The relative proportions of the lower premolars seem to be higher in the type species, than in the Hammerschmiede hemimandibles (Table 3). The morphological comparison is made based on the material published by Pilgrim (1932), Morales and Pickford (2005b) and Grohé et al. (2020). The upper carnassial of *V. chinjiensis* is more slender than that of *V. neptuni* sp. nov., with a less developed hypocone (both in width and in height), a fainter cingulum and a considerably smaller parastyle. The lower dentition of the two species is very similar. However, the m1 metaconid is relatively lower in *V. chinjiensis* and the talonid is wider than the trigonid. The lower carnassial of this species lacks the notch between the distal cristid of the protoconid and the mesial cristid of the hypoconid.

TABLE 3. Comparison of the relative lengths of the lower premolars in relation to m1L in *Vishnuonyx neptuni* sp. nov. with other species of *Vishnuonyx*. Data from: Grohé et al. (2020).

Species	Code	p2L/ m1L	p3L/ m1L	p4L/ m1L
Vishnuonyx neptuni sp. nov.	GPIT/MA/16733	35.4	44.2	60.5
	BSPG 2020 XCIV-0301	40.4	44.7	63.8
	BSPG 2020 XCIV-1301			62.4
Vishnuonyx chinjiensis	GSP-Y 40764		52.5	70.3
Vishnuonyx maemohensis	MM-30 left	44.5	51.3	68.9
	MM-32			71.7
	MM-33	48.6	50.5	63.8
	MM-34		46.8	69.4
	MM-35			66.4

Similarly, *V. maemohensis* is smaller than *V. neptuni* sp. nov. (Tables 1 and 2), while its premolars are relatively longer (Table 3). The morphological comparisons are based on the specimens published by Grohé et al. (2020). The P3 of the Thai species is very similar to that from Hammerschmiede, but the lingual root of the tooth is partially fused to the distal root. However, this trait, based on the slenderness of the lingual root, can be considered as an abnormality (Fig. 2). The upper carnassial is more slender than that from Hammerschmiede, with a less developed hypocone (both in width and height), less robust cingulum and a smaller parastyle. The M1 morphology of *V. maemohensis* is very similar to that of *V. neptuni* sp. nov., but, apart from the size difference, it lacks a protoconule, the paraconule and metaconule are considerably smaller, the labial expansion of the paracone area is less enhanced and the lingual platform is relatively more reduced. The lower teeth of *V. maemohensis* exhibit a distinct outline compared with the ones of *V. neptuni* sp. nov., due to their blunt and convex ridges that create a more robust profile. The mental foramen in *V. maemohensis* is located below p3, in contrast to that of *V. neptuni* sp. nov., which is located below p2, while the p3 is lower and blunter in the Thai species. Additionally, the lower carnassial in *V. maemohensis* lacks the notch between the distal cristid of the protoconid and the mesial cristid of the hypoconid.

The species *V.*? *angololensis* is known only by an upper carnassial from the Lower Nawata Formation in Lothagam (Werdelin, 2003). The metrical comparison exhibits that this specimen is considerably larger than the P4 from Hammerschmiede (Table 1). In terms of morphology, the African specimen does not have a parastyle, the hypocone is smaller than the protocone, the protocone is situated more mesially (reaching the level of the mesial border of the tooth), and the cingulum is less prominent in the mesiolabial side of the paracone and the distal end of the metastyle.

A fragmentary hemimandible assigned to *Vishnuonyx* sp. by Haile-Selassie (2008), from the lower Pliocene of the Haradaso Member of the Middle Awash, Ethiopia, differs from *V. neptuni* sp. nov. in having a more robust m1.

Thus, both overall morphology and dental proportions of the specimens from Hammerschmiede differ from all the known forms of *Vishnuonyx*, and accordingly the erection of *V. neptuni* sp. nov. is well justified.

Paleobiogeography

The new taxon described herein is of great interest, not only in terms of taxonomy, but also in terms of paleobiogeography. The record of the genus *Vishnuonyx* is characterized by sporadic occurrences in East Africa and Southern Asia (Thailand and the Indian subcontinent), while *V. neptuni* sp. nov. represents the westernmost and northernmost occurrence and the first European representative of the genus (Fig. 1). The Asian record of the genus includes its oldest known occurrence in the Middle Miocene (14.2–13.2 Ma) from Mae Moh in Thailand (Grohé et al., 2020), but also the slightly younger Middle Miocene (13.8–12.7 Ma) material from the Siwaliks, India (Pilgrim, 1932; Sehgal, 2013; Grohé et al., 2020). In Africa, the genus seems to have a stratigraphically longer fossil record from the late Middle Miocene at 12 Ma (Loc. 2/11 of Ngorora

D; *V. chinjiensis*; Morales and Pickford, 2005b) to the Late Miocene (Lower Nawata, Lothagam; 7.3–6.6 Ma, Böhme et al., 2021; *V.*? *angololensis*; Werdelin, 2003) and finally to the earliest Pliocene (Haradaso; 5.2–4.85 Ma; *Vishnuonyx* sp.; Haile-Selassie, 2008). The age of the HAM 4 fossiliferous layer (11.44 Ma; Kirscher et al., 2016) is slightly younger than the records from Siwaliks and Ngorora D.

Considering the oldest known record of *Vishnuonyx* from Thailand as the most ancestral in its evolutionary line (in terms of morphology and biogeography), the radiation of the genus from Southeast Asia towards the Indian subcontinent, East Africa and Europe was completed by the end of the Middle Miocene. Particularly, the radiation event from southern Asia to Africa (where the genus persisted until the early Pliocene) occurred before 12 Ma (Grohé et al., 2020). Similarly, if the significant morphological differences of *V. neptuni* sp. nov. from the other species of the genus are considered, a relatively long period of genetic isolation seems justified. Therefore, we consider that the dispersal of *Vishnuonyx* to Europe must be noticeably older than 11.5 Ma.

Given the supposed semi-aquatic lifestyle of *Vishnuonyx*, the dispersal path of this otter must be searched for in a water connection between South Asia, East Africa, and Central Europe. The lutrines are a group that lives in proximity to both seawater and fresh water (e.g., Hung and Law, 2016), while some taxa, like *Enhydra lutris* (Linnaeus, 1758), are primarily marine (Estes, 1980). Therefore, the pathway of the genus between South Asia and Europe could possibly include either seawater or fresh water. Thus, the biogeography of *Vishnuonyx* can be understood considering marine gateways.

A marine water connection between these two regions was potentially present during the Konkian Eastern Paratethys regional chronostratigraphic stage (late Badenian, early Serravalian; 13.4–12.65 Ma; Palcu et al., 2017). During the Konkian, the Eastern Paratethys was connected to the Central Paratethys (Studencka et al., 1998; Kovac et al. 2007; Palcu et al., 2017) and, via the Araks Strait, probably to the Eastern Mediterranean and the Mesopotamian Basin (Fig. 4). The existence of the Araks Strait has been proposed on the basis of marine benthos (echiniids, scaphopods, gastropods, bivalves) found in Konkian sediments of the southeastern part of the Eastern Paratethys (see Studencka et al., 1998 and Iljina, 2003 for discussion and references). However, it remains yet unresolved if this gateway connects the Eastern Paratethys only to the Eastern Mediterranean via northern Syria or in addition via the Mesopotamian Basin to the Indian Ocean (Rögl 1998, 1999; Popov et al., 2004, Palcu et al., 2017). However, the last possibility is supported by Indo-Pacific affinities of late Badenian Radiolaria (Dumitrică 1978). Furthermore, the terminal marine influence in the Mesopotamian Basin, marked by the top of the marine Lower Fars, respectively Gahsaran Formations, has been dated in the Zagros foreland to 12.3 Ma (Homke et al., 2004; Böhme et al., 2021). In any case, a marine dispersal of *Vishnuonyx* from Asia to Europe via Mesopotamia could have happened only around 13 Ma during the Konkian, since the Araks Strait was closed before 13.4 (Karaganian regional stage) and after 12.65 Ma (Volhynian regional stage) (Studencka et al. 1998).

This approach, concerning the dispersal path of *Vishnuonyx* towards Central Europe, fits very well with the age of Hammerschmiede, the degree of differentiation in morphology, as well as the combination of the otter semi-aquatic lifestyle and the potential water connection between the Mesopotamian Basin and the Paratethys around 13 Ma. Similarly, a possibly

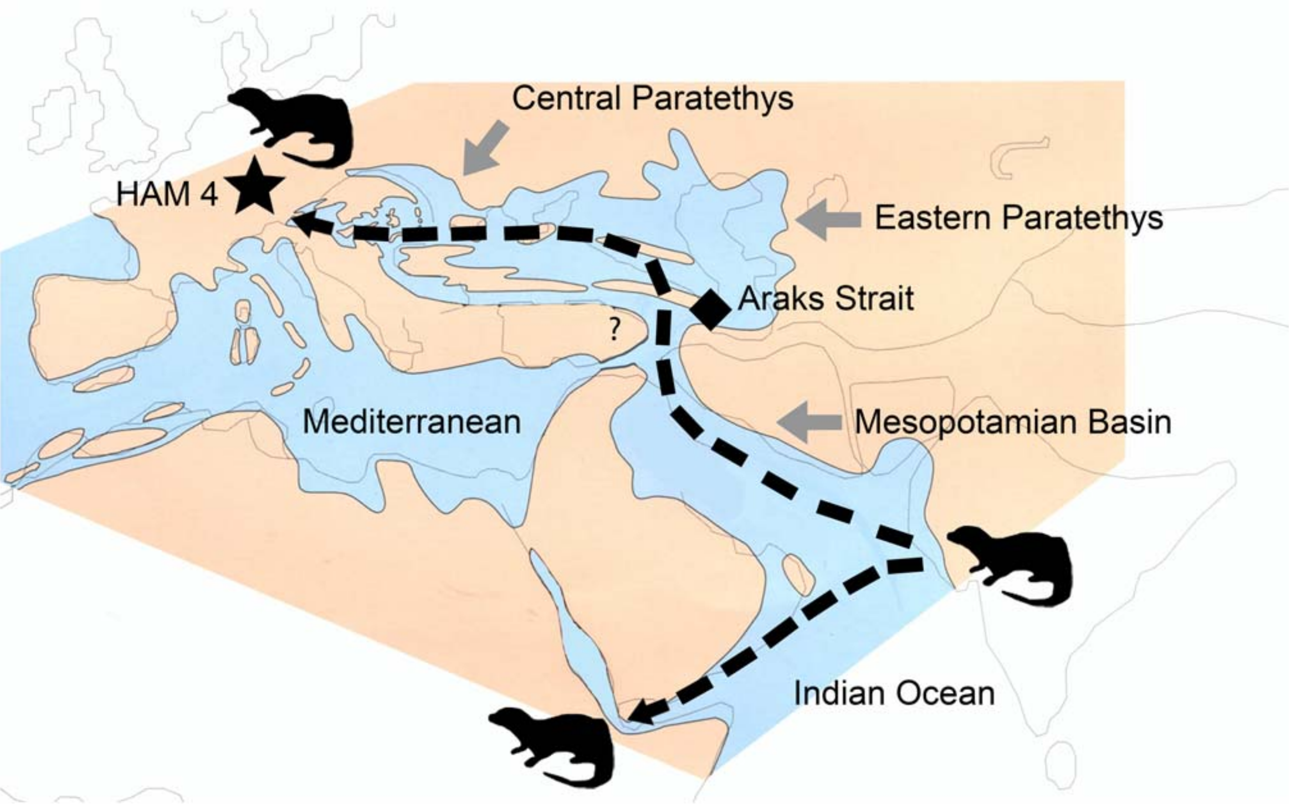

FIGURE 4. The proposed dispersal path of *Vishnuonyx* from South Asia towards Central Europe and East Africa during the Konkian around 13 Ma (late Badenian, early Serravalian). Modified after Rögl (1998) and Popov et al. (2004).

contemporaneous dispersal along the northwestern shorelines of the Indian Ocean into the East African Rift seems plausible.

Dietary Specialization of *Vishnuonyx*

Overall, the jaws and teeth of lutrines are adapted to fulfill two tasks: catching slippery fish and crushing hard items (such as bivalves or crustaceans), and all the extant members of the subfamily feed on both types of food (Friscia et al., 2006; Christiansen and Wroe, 2007). However, the percentages between the two types can fluctuate significantly and this variability can be correlated with the morphology of the post-canine dentition. Commonly, crushing bivalves requires a large occlusal area with several cusps that can create cracks in the shells (e.g., Lucas, 1979; Popowics, 2003; Friscia et al., 2006; Constantino et al., 2011; Hartstone-Rose, 2011). Conversely, catching fish inside the water requires pointy, blade-like teeth that can hang on to the prey (Lucas, 1979; Popowics, 2003; Friscia et al., 2006; Hartstone-Rose, 2011). Some extant lutrines exhibit adaptations that tend more to the former morphology (e.g., the Aonychini or *Enhydra*), while others to the latter (e.g., *Lutra* Brünnich, 1772, *Lontra* Schreber, 1777 or *Pteronura* Gray, 1837) (e.g., Willemsen, 1992; Popowics, 2003; Friscia et al., 2006). In fact, cases of extant otters of these two ecological groups living in the same region have been recorded. A fine example of this dietary partition has been reported from Thailand, where the extant *Lutra perspicillata* (Geoffroy Saint Hilaire, 1826) and *Lutra lutra* (Linnaeus, 1758) are feeding mainly on fish and amphibians, whereas *Aonyx cinereus* (Illiger, 1815) is particularly specialized on crabs (Kruuk et al., 1994). Following this ecomorphological distinction between more piscivorous and more durophagous otters, the teeth of *V. neptuni* sp. nov. seem to be better adapted to the former. Several traits point towards this direction: the mesiodistally narrow M1, the pointed premolars with high and curved main cuspids, the developed accessory cuspid in p4, the high m1 trigonid cusps, the narrow and short m1 talonid, the restricted m1 talonid cusps and the presence of a carnassiform notch between the distal cristid of the protoconid and the mesial cristid of the hypoconid (Crusafont-Pairó and Truyols-Santonja, 1956; Lucas, 1979; Van Valkenburgh, 1989; Van Valkenburgh and Koepfli, 1993; Popowics, 2003; Friscia et al., 2006; Hartstone-Rose, 2011). Additionally, the lower carnassial of SNSB-BSPG 2020 XCIV-0301 exhibits significant horizontal wear in its carnassial blade while the talonid is almost unworn. These hints suggest a diet based mostly on soft tissue/flesh (in that case fish) and less on hard material such as bivalves, crustaceans, or plants (Van Valkenburgh, 1989; Gipson et al., 2000; DeSantis et al., 2017; Schultz et al., 2020). However, extant lutrines exhibit a wide range of diet preferences and no definite suggestions can be made without a multiproxy approach.

Therefore, the attribution of *Vishnuonyx* spp. to the group of bunodont otters is not supported in an ecological sense. On the contrary, it shares several similarities with the living giant otter *Pteronura brasiliensis* (Zimmermann, 1780): strong P4, reduced M1, pointed lower premolars and relatively strong m1. *Pteronura* feeds mostly on fish (Noonan et al., 2017), supporting the indication of a comparable dietary specialization for *Vishnuonyx*.

CONCLUSIONS

The lutrine material from Hammerschmiede published herein, represents a new species of the genus *Vishnuonyx*, *V. neptuni* sp. nov. This record is the westernmost and northernmost occurrence of the genus and the first in Europe. The dispersal event of this South Asian otter is proposed to have happened during the Konkian (13.4–12.65 Ma) through a water connection between the Mesopotamian Basin and the Eastern Paratethys. The dietary specialization of *V. neptuni* sp. nov. is suggested to be focused more on piscivory and less on durophagy.

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