PLEISTOCENE LANG TRANG FAUNA IN NORTH VIETNAM: TAXONOMIC COMPOSITION AND HABITATS

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1. INTRODUCTION

The systematic studies of the Pleistocene fauna of terrestrial vertebrates in northern Vietnam began in the 1960s, when the researches of the Vietnamese-German expedition led by H.D. Kahlke discovered more than ten cave sites with remains of mammals [1]. The Lang Trang cave complex, located on the right bank of the Ma River on the west of Thanh Hoa Province, Ba Thuoc District, near Canh Nang town (20°20′29″ N, 105°12′21″ E), was among those sites. The first data on the composition of mammal assemblage of the locality in addition to paleoanthropological and archaeological data were published [2, 3] in the results of 1988-1989 excavations by the Vietnamese-American expedition. Since 2020, the excavations in the Lang Trang cave were carried out by Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN) and Institute of Tropical Ecology of the Joint Vietnam - Russia Tropical Science and Technology Research Center within the framework of the paleoecological studies of the Tropical Center (Project "The Composition of the Fauna of Primates (Cercopithecidae, Pongidae) and Rodents (Rodentia) of the Pleistocene and Holocene of Vietnam as an Indicator of Environmental Change").

2. MATERIALS AND METHODS

New data obtained by the Russian-Vietnamese expeditions in 2020-2022 significantly expanded our understanding of the taxonomic composition of the Lang Trang fauna (Table 1) and the environments in the region, and also clarified the age of the locality as the beginning of the Late Pleistocene [4÷10].

Table 1. Taxonomic composition of the Pleistocene fauna in the Lang Trang cave

Ciochon and Olsen [3]	Long et al. [3], Bacon et al. [11] (*)	Lopatin [4, 5, 6, 7], Lopatin et al. [8, 9, 10], and new data herein (**)
Primates *Homo* sp., *Pongo pygmaeus* ssp., *Hylobates* sp., *Presbytis* sp., *Macaca arctoides*, *M. mulatta*, *Macaca* sp.	**Primates** *Pongo pygmaeus*, *Hylobates* sp., *Presbytis / Trachypithecus* sp., *Macaca* sp.	**Primates** *Gigantopithecus blacki*, *Pongo* sp., *Hylobates* sp.**, *Trachypithecus* sp., *Pygathrix* sp.**, *Presbytis* sp., *Macaca nemestrina*, *M.* cf. *fascicularis*, *M.* cf. *mulatta*, *Macaca* sp.
Carnivora *Ursus malayanus*, *U. thibetanus*, *Ailuropoda melanoleuca*, *Arctonyx collaris*, cf. *Melogale moschata*, cf. *Paguma larvata*, cf. *Paradoxurus hermaphroditus*, cf. *Viverra* sp., *Cuon antiquus*, cf. *Canis* sp., *Panthera tigris*, cf.	**Carnivora** *Ursus malayanus*, *U. thibetanus*, *Ailuropoda melanoleuca*, *Arctonyx collaris*, *Lutra perspicillata*, *Paradoxurus hermaphroditus*, *Cuon*	**Carnivora** *Arctonyx collaris rostratus*, *Panthera tigris*, *Neofelis nebulosa*

Ciochon and Olsen [3]	Long et al. [3], Bacon et al. [11] (*)	Lopatin [4, 5, 6, 7], Lopatin et al. [8, 9, 10], and new data herein (**)
P. pardus, *Felis temmincki*	*javanicus*, *Panthera tigris*, *P. pardus*, *Felis temmincki*	
Proboscidea *Elephas namadicus*, *Stegodon orientalis*	**Proboscidea** *Elephas maximus / namadicus*, *Stegodon orientalis*	**Proboscidea** *Elephas maximus*, *Stegodon* sp.
Perissodactyla *Tapirus (Megatapirus) angustus*, *Rhinocerus sinensis*	**Perissodactyla** *Tapirus indicus*, *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus**	**Perissodactyla** *Tapirus indicus*, *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus***, *Rhinoceros unicornis***
Artiodactyla *Sus scrofa*, *Tragulus* cf. *javanicus*, *Muntiacus muntjak*, *Cervus (Rusa) unicolor*, *Cervus* sp., *Capricornis sumatraensis*, *Bos (Bibos) gaurus*, *Bos* sp.	**Artiodactyla** *Sus scrofa*, *Muntiacus muntjak*, *Rusa unicolor*, *Capricornis sumatraensis*, *Bubalus bubalis*	**Artiodactyla** *Sus scrofa*, *S. barbatus*, *Tragulus kanchil*, *Hydropotes inermis*, *Muntiacus muntjak*, *Axis porcinus*, *Rusa unicolor*, *Capricornis sumatraensis*, *Bubalus arnee***, *Bos* sp.**
Rodentia *Hystrix subcristata*, *Atherurus macrourus*, *Rhizomys troglodytes*, *Rattus sabanus*	**Rodentia** *Hystrix brachyura*, *Atherurus macrourus*, *Rattus sabanus*	**Rodentia** *Hystrix kiangsenensis*, *Leopoldamys neilli*, *Rattus rattus*
Chiroptera Family indet.		**Chiroptera** *Ia io*
		Lipotyphla *Chodsigoa hoffmanni*
		Crocodilia *Crocodylus* sp.
		Testudines *Cuora* sp.**
Gastropoda *Cyclophorus* sp.		**Gastropoda** *Pollicaria rochebruni*, *Cyclophorus fasciatus*, *Cyclophorus* sp., *Rhiostoma morleti*, *Brotia jullieni*, *Sulcospira* cf. *collyra*, *Ellobium aurismidae*, *Megalauchenia proctostoma*, *Camaena* cf. *vanbuensis*

The macroscopic investigation of the fossil-bearing sediments was carried out in the field, while the microscopic analysis was done in the laboratory [10].

The collected paleontological materials were studied at the PIN, Moscow. The fossil measurements were made using a digital caliper with 0.01 mm precision and an ocular micrometer on the Leica MZ6 stereo microscope with 0.05 mm precision. Illustrations were made using the Nikon D800 digital photo camera with an AF-S Micro NIKKOR 60mm f/2.8G ED lens and Canon EOS 7D Mark II digital photo camera with EF 100mm f/2.8 Macro USM lens.

3. RESULTS AND DISCUSSION

Various representatives of the *Stegodon-Ailuropoda* Fauna characterizing the second half of the Middle - early Late Pleistocene of Southeast Asia were identified in the materials collected by the Joint Vietnam - Russia Tropical Science and Technology Research Center (totally more than 700 specimens), namely: primates *Gigantopithecus blacki* von Koenigswald, 1935, *Pongo* sp., *Trachypithecus* sp., *Presbytis* sp., *Macaca nemestrina* (Linnaeus, 1766), *M.* cf. *fascicularis* Raffles, 1821, *M.* cf. *mulatta* (Zimmermann, 1780), and *Macaca* sp., carnivorans *Panthera tigris* (Linnaeus, 1758), *Neofelis nebulosa* (Griffith, 1821), and *Arctonyx collaris rostratus* Matthew et Granger, 1923, lipotyphlan *Chodsigoa hoffmanni* Chen et al., 2017, bat *Ia io* Thomas, 1902, rodents *Hystrix kiangsenensis* Wang, 1931, *Leopoldamys neilli* (Marshall, 1976), and *Rattus rattus* (Linnaeus, 1758), proboscideans *Stegodon* sp., and *Elephas maximus* Linnaeus, 1758, perissodactyls *Tapirus indicus* (Desmarest, 1819), *Dicerorhinus sumatrensis* (Fischer, 1814), *Rhinoceros sondaicus* Desmarest, 1822, and *R. unicornis* Linnaeus, 1758, artiodactyls *Sus scrofa* Linnaeus, 1758, *S. barbatus* Müller, 1838, *Tragulus kanchil* (Raffles, 1821), *Hydropotes inermis* Swinhoe, 1870, *Muntiacus muntjak* (Zimmermann, 1780), *Axis porcinus* (Zimmermann, 1780), *Rusa unicolor* (Kerr, 1792), *Capricornis sumatraensis* (Bechstein, 1799), *Bubalus arnee* (Kerr, 1792), and *Bos* sp., as well as crocodiles, turtles, and representative gastropod assemblage (Figs 1, 2).

Gigantopithecus blacki, *Macaca* cf. *fascicularis*, *M.* cf. *mulatta*, *Neofelis nebulosa*, *Chodsigoa hoffmanni*, *Ia io*, *Leopoldamys neilli, Rattus rattus*, *Rhinoceros unicornis*, *Sus barbatus*, *Tragulus kanchil, Hydropotes inermis*, *Axis porcinus*, crocodiles, turtles and most of the gastropod species were identified for the first time in the Lang Trang fauna.

The primate remains from the Lang Trang locality compose a significant portion in the finds of 2020-2022 (ca. 100 specimens). The representatives of four families are recorded, i.e.: Hominidae (*Gigantopithecus blacki*, 2 specimens; *Pongo* sp., 17 specimens), Hylobatidae (*Hylobates* sp., 4 specimens), Cercopithecidae (47 specimens), and Colobidae (27 specimens).

The find of a giant ape, *Gigantopithecus blacki* [9], is of special importance. It is the first finding in the Upper Pleistocene of Vietnam, as well as the latest one in the fossil record (ca. 125 ka BP). The data on geographic and stratigraphic distribution of *G. blacki* indicate that the range of this species in the Middle Pleistocene was reduced to a small area in southern China and northern Vietnam. Apparently, the extinction of this giant ape corresponds to the Middle - Late Pleistocene transition, so that the specimens from the Lang Trang cave (Fig. 1a) belong to one of the latest relict populations of *G. blacki*.

Judging from the morphology and size of the upper and lower teeth, the orangutan from the Lang Trang cave (Fig. 1b) was previously assigned to the fossil subspecies *Pongo pigmaeus ciochoni* Schwartz et al., 1995 [12]. However, the recent orangutan *P. pigmaeus* is characterized by a high polymorphism in the tooth structure; therefore, the subspecies status of the Lang Trang form remains the subject of discussion.

The material on *Hylobates* sp. includes well-preserved M1 (Fig. 1c) of typical morphology (measurements in mm, specimen PIN, no. 5792/21: maximum length, L, 7.2; maximum width, W, 7.2).

The cercopithecoid monkeys compose the largest group of primates in the locality, among them the colobids are 28 %, whereas the cercopithecids are 72 %. The southern pig-tailed macaque, *Macaca nemestrina*, with largest teeth within the family members from the locality, is the most common among the Cercopithecidae. In addition, other two relatively small members of the genus were found. The larger form was determined as *M*. cf. *mulatta*, the smaller one - as *M*. cf. *fascicularis*. Most likely, there is another one macaques species in the locality, but due to the lack of material, it is identified as *Macaca* sp. The Colobidae family is represented by small *Trachypithecus* sp., *Pygathrix* sp., and the larger *Presbytis* sp.

The carnivorans remains are rare, isolated teeth of the greater hog badger *Arctonyx collaris rostratus* (Mustelidae) predominate among them. The Lang Trang population of this extinct subspecies is characterized by large sizes of molars, which, in terms of maximum length and width, somewhat exceed the corresponding parameters established for the Chinese populations (Fig. 1k) [5, 10]. The isolated teeth of felines have also been found, i.e. the tiger *Panthera tigris* and the clouded leopard *Neofelis nebulosa* (Figs 1f, 1g, 1j) [10]. The new finds include penultimate upper premolar of *P. tigris* (specimen PIN, no. 5792/223, P3: L, 21.6; W, 10.6) and the upper canine fragment of *N. nebulosa* (specimen PIN, no. 5792/624) with typical flattened shape and paired deep narrow grooves along the lateral sides (Figs 1d, 1e, 1h, 1i).

The proboscidean remains from the Lang Trang locality are represented by tooth fragments of Elephantidae and Stegodontidae. Three determinable fragments of the upper teeth of an Asian elephant, *Elephas maximus*, are among them: specimen PIN, no. 5792/528 (isolated M1 plate); specimen PIN, no. 5792/339 (isolated DP3 plate); specimen PIN, no. 5792/712 (fragment of DP4). The morphological and morphometric characteristics of the teeth of the Asian elephant from Lang Trang (Table 2) slightly differ from the corresponding characteristics of recent elephants from Vietnam [13]. Compared to recent members of the species, the Asian elephant from Lang Trang has a relatively wider crown; there is no difference in the thickness of the enamel. We do not confirm the presence of *E. namadicus* [2, 3] in the Lang Trang locality.

Table 2. The morphological and morphometric characteristics of the upper teeth of the third (DP4) and forth (M1) replacements in *Elephas maximus* from South Vietnam, Gia Lai Province (Recent) and Lang Trang locality (early Late Pleistocene)

Locality	Crown height / width, mm	Enamel thickness, mm	Crown height / width ratio, %
Lang Trang, specimen PIN, no. 5792/712, DP4	~112.0/~58.0	1.1	51.7
Gia Lai Province, Côn River, specimen PIN, no. 5487/9, DP4 [13]	94.5/52.0	1.2	55.0
Lang Trang, specimen PIN, no. 5792/528, M1	135.0/84.0	1.8	62.0
Gia Lai Province, Côn River, specimen PIN, no. 5487/3, M1 [13]	123.0-124.3/53.5	1.4-1.8	44.0

Stegodon sp. is another representative of Proboscidea in Lang Trang. Due to the poor preservation of the tooth fragments, it can be determined only to the genus level. It is noted that *Elephas* and *Stegodon* repeatedly succeeded each other at different chronological intervals in the *Stegodon-Ailuropoda* Fauna of southern China and northern Thailand during the Middle and Late Pleistocene [14]. The species *Stegodon orientalis* Owen, 1870 is characteristic for the boundary of the Middle and Late Pleistocene in Southeast Asia [14], in Thailand it also occurs together with *Elephas* sp. [15]. In a number of studied localities of northern Vietnam, including Lang Trang, *Stegodon* and *Elephas* were found together (our data).

Perissodactyls are represented by tapirs and rhinoceroses in the Lang Trang assemblage. Remains of the Malayan tapir, *Tapirus indicus*, include several isolated teeth (Fig. 1m). The species occurred in southern China during the Early Pleistocene, in Thailand, Cambodia, Laos, and on Java in the Middle Pleistocene, in Laos, Vietnam, Malay Peninsula, Borneo, Sumatra, and Java in the Late Pleistocene [15, 16].

Over 30 definable upper and lower teeth of three rhinoceros species are present in the materials collected in 2020-2022 (Figs 1n-1r). Judging from the size and structure, a part of them represents Sumatran rhinoceros, *Dicerorhinus sumatrensis*, the least among modern Rhinocerotidae species (specimen PIN, no. 5792/410, m1: L, 37.0; W, 18.5; specimen PIN, no. 5792/38, m2: L, 39.5; W, 23.6; specimen PIN, no. 5792/28, m3: L, 46.0; W, 26.6). Its fossils are known from the Lower Pleistocene of Myanmar, the Middle Pleistocene of southern China, the Upper Pleistocene of Vietnam, Malay Peninsula, Sumatra, Borneo and Java [15, 16].

The larger form remains were discovered in the Lang Trang cave in 2022 (for instance, specimen PIN, no. 5792/671, P2: L, 33.0; W, 33.4; specimen PIN, no. 5792/703, M2: L, 44.0; W, 46.0; specimen PIN, no. 5792/589, p2: L, 28.5; W, 17.0; specimen PIN, no. 5792/416, p3: L, 33.5; W, 21.0; specimen PIN, no. 5792/412, m2: L, 49.5; W, 29.0; specimen PIN, no. 5792/22, m3: L, 46.5; W, 29.3). The data analyze on the size variability of the teeth of different species of Southeast Asian rhinoceroses [15, 17] allows us to conclude that they belong to the Javan rhinoceros, *Rhinoceros sondaicus*.

The remains of an even larger form (specimen PIN, no. 5792/25, p3: L, 42.5; W, 20.5; specimen PIN, no. 5792/636, m1: L, 47.0; W, 21.5) can be attributed to the Indian rhinoceros, *Rhinoceros unicornis*.

The co-occurrence of *D. sumatrensis, R. sondaicus*, and *R. unicornis* has also been noted for other localities of northern Vietnam dating as the transition from the Middle to the Late Pleistocene, MIS6-5, 148-117 ka BP [18].

Ten species of artiodactyls have been identified in the Lang Trang fauna [8, 10], including representatives of the families Suidae (*Sus scrofa*, *S. barbatus*), Tragulidae (*Tragulus kanchil*), Cervidae (*Hydropotes inermis*, *Muntiacus muntjak*, *Axis porcinus*, *Rusa unicolor*), and Bovidae (*Capricornis sumatraensis*, *Bubalus arnee*, and *Bos* sp.).

The wild boar, *Sus scrofa*, has been recorded in Southwest Asia since the Early Pleistocene [3]. The bearded pig, *S. barbatus*, as a fossil was found in the Middle and Upper Pleistocene of Thailand, the Upper Pleistocene of Vietnam, Laos, Malaysia, and Indonesia, including Sumatra, Java, and Borneo; in a number of localities, like the Lang Trang cave, it co-occurred with a wild boar [3, 11, 15]. The Lesser oriental chevrotain, *Tragulus kanchil*, a member of the archaic Tragulidae family, inhabits the tropical forests of Southeast Asia, in modern days ranges from ca. 18° N latitude south to Sumatra, Borneo and the Sunda Isles. This species is represented by a single find [8]. The water deer, *Hydropotes inermis*, was also identified from a single finding of a tooth with a characteristic structure [8]. Nowadays this species occurs in the east of China (in the Yangtze River basin) and in Korea. It has been known since the Early Pleistocene in China, but in Southeast Asia it was discovered for the first time. The hog deer, *Axis porcinus*, represented in the Lang Trang locality by a few remains, has been known in Southeast Asia since the Middle Pleistocene. The remains of the southern red muntjac, *Muntiacus muntjak*, the sambar deer, *Rusa unicolor*, and the serow, *Capricornis sumatraensis*, are more numerous. The larger deer, muntjac and sambar, have been widely represented on the continental part of Southeast Asia since the Middle Pleistocene, and in the Late Pleistocene they settled on the Greater Sunda Isles [15]. The serow, nowadays inhabiting mountains from Eastern Tibet and Northern India to South China and Southeast Asia (as far as Sumatra), has been known in China since the Early Pleistocene, and in Southeast Asia from the Middle Pleistocene [3, 15]. In 2022 finds from the Lang Trang the large bovid are represented by two forms, *Bubalus arnee* and *Bos* sp. (Figs 1s-1v).

The artiodactyl assemblage of the Lang Trang is similar to the Laos and Thailand communities dated as the end of the Middle - beginning of the Late Pleistocene [8, 10]. Its taxonomic composition supports possible zoogeographic relationships both with the Pleistocene faunas of Pakistan and India, and with the faunas of South China. Along with the autochthonous forms (*Sus barbatus* and *Tragulus kanchil*), there are species that could have spread to the studied region from the west or north (*Axis porcinus*, *Muntiacus muntjak*, *Rusa unicolor*,

Capricornis sumatraensis), and from the north (*Hydropotes inermis*). In general, the dwellers of a variety of tropical forests (from lowland to mountain) predominate, there are inhabitants of wet biotopes, including rivers floodplains and coastal plains (*A. porcinus*, *H. inermis*, *Bubalus arnee*), as well as mangroves (*T. kanchil*, *S. barbatus*). Some species are adapted to drier landscapes (*C. sumatraensis*) or occur in a relatively wide range of habitats (*S. scrofa, R. unicolor*) [8, 10].

The large porcupine, previously identified as *Hystrix brachyura* Linnaeus, 1758 or *H. indica* Kerr, 1792, is known from Lang Trang cave by numerous isolated teeth. Based on the analysis of morphometric data, the systematic position of this form is redefined as *H. kiangsenensis* (Fig. 1l) [6, 10]. Probably, this extinct species was the main agent of bioerosion of the mammal bone remains in the Lang Trang cave (many bone fragments of bones and tooth roots bear signs of osteophagy that is characteristic of porcupines); apparently, the porcupines participated in the bones accumulation in the cave cavities.

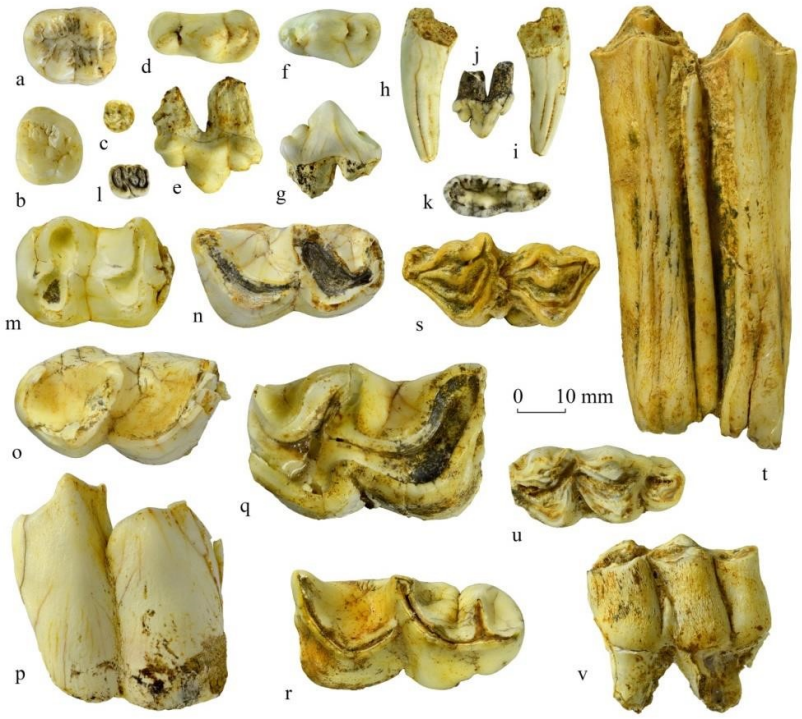

Fig. 1. Mammals from the Lang Trang locality: (a) *Gigantopithecus blacki* von Koenigswald, 1935, specimen PIN, no. 5792/439, right m2, occlusal view; (b) *Pongo* sp., specimen PIN, no. 5792/7, left M3, occlusal view; (c) *Hylobates* sp., specimen PIN, no. 5792/21, left M1, occlusal view; (d-g) *Panthera tigris* (Linnaeus, 1758): (d, e) specimen PIN, no. 5792/223, left P3, occlusal (d) and labial (e) views; (f, g) specimen PIN, no. 5792/230, right p4, occlusal (f) and labial (g) views; (h-j) *Neofelis nebulosa* (Griffith, 1821): (h, i) specimen PIN, no. 5792/624, left C1, labial (h) and lingual (i) views; (j) specimen PIN, no. 5792/236, right P3, labial views; (k)

Arctonyx collaris rostratus Matthew et Granger, 1923, specimen PIN, no. 5792/231, right m1, occlusal view; (l) *Hystrix kiangsenensis* Wang, 1931, specimen PIN, no. 5792/406, left M1, occlusal view; (m) *Tapirus indicus* (Desmarest, 1819), specimen PIN, no. 5792/4, left m2, occlusal view; (n-p) *Dicerorhinus sumatrensis* (Fischer, 1814): (n) specimen PIN, no. 5792/38, right m2, occlusal view; (o, p) specimen PIN, no. 5792/28, left m3, occlusal (o) and labial (p) views; (q) *Rhinoceros sondaicus* Desmarest, 1822, specimen PIN, no. 5792/22, left m3, occlusal view; (r) *Rhinoceros unicornis* Linnaeus, 1758, specimen PIN, no. 5792/636, right m1, occlusal view; (s, t) *Bubalus arnee* (Kerr, 1792), specimen PIN, no. 5792/670, left m2, occlusal (s) and labial (t) views; (u, v) *Bos* sp., specimen PIN, no. 5792/691, left m3, occlusal (u) and labial (v) views; Vietnam, Thanh Hoa Province, Ba Thuoc District, Lang Trang cave; lower Upper Pleistocene.

Other rodents are represented by two species of Muridae, i.e. *Leopoldamys neilli* and *Rattus rattus* [10]. Both species occur at present in Vietnam.

The bat *Ia io* nowadays inhabits Nepal, East India, South China, Thailand, Myanmar, Laos, and Vietnam. It is known from the Pleistocene of China, but in Vietnam it was discovered as a fossil for the first time [4]. The material from the Lang Trang cave is represented by a dentary fragment.

The maxillary fragment of shrew *Chodsigoa hoffmanni* from the Lang Trang cave [7] is the first fossil find of the species that occurs now in Ha Giang Province in northern Vietnam and in Yunnan, Guizhou, and Hubei provinces of China.

The size of the tooth of *Crocodylus* sp. from the Lang Trang cave [10] corresponds to an individual with a body length of at least 1.5 m. Currently, two species of crocodiles live in Vietnam, i.e. Siamese crocodile, *C. siamensis* Schneider, 1801, and saltwater crocodile, *C. porosus* Schneider, 1801. They occurs in the lowland southern part of the country with a smooth tropical climate, and are absent in the northern regions. The presence of a crocodile in the Lang Trang fauna indicates the existence of a large permanent water body or a slow flowing river near the cave and does not exclude the proximity of the sea shore (*C. porosus* now commonly inhabits sea coasts, mangrove swamps, and river deltas).

In 2022, the remains of *Cuora* sp., a geoemydid turtle, were found in the Lang Trang cave. The modern members of the family live in tropical and subtropical freshwater, as well as in sea coasts and tropical forests ecosystems. The species of the genus *Cuora* are widely distributed in Southeastern Asia, including several species in Vietnam. These turtles prefer shallow, densely overgrown swamps and river dams. The fossil representatives of the genus are known from the Late Miocene to the Holocene of China, Japan, and Thailand [19]. *Cuora* sp. from the Lang Trang cave is the first fossil find of the Asian box turtles in Vietnam.

The mollusk assemblage from the Lang Trang cave includes recent species that nowadays occur in northern Vietnam and represents a mixture of terrestrial, freshwater and coastal marine forms (Fig. 2). The following species are determined

in the assemblage: terrestrial *Pollicaria rochebruni* (Mabille, 1887), *Cyclophorus fasciatus* Kobelt, 1908, *Cyclophorus* sp., *Rhiostoma morleti* (Dautzenberg et Fischer, 1906), *Megalauchenia proctostoma* (Mabille, 1889), and *Camaena* cf. *vanbuensis* Smith, 1896, freshwater *Brotia jullieni* (Deshayes, 1874) and *Sulcospira* cf. *collyra* Köhler et al., 2009, and shallow water marine species *Ellobium aurismidae* (Linnaeus, 1758). *E. aurismidae* is widely distributed along the coastal regions of the Western Pacific (Vietnam, Thailand, Philippines, Malaysia, Indonesia, and south to northern Australia), where it frequents coastal mangroves and river estuaries, living in grass on mudflats, as well as on the roots and trunks of mangroves and *Nypa* mangrove palms in the littoral and supralittoral zones [10]. The presence of this species makes possible to synchronize the time of accumulation of the studied deposits with the episode of the largest marine transgression in the Late Pleistocene (MIS 5e, ca. 125 ka BP) [20], when the sea line has approached the cave area (currently, the Lang Trang cave is over 90 km away from the sea coast, and about 60 m above the sea level). The finds of terrestrial mollusks, *Pollicaria, Cyclophorus, Rhiostoma, Megalauchenia, and Camaena*, in the assemblage can be explained by their transportation from the elevated areas by streams and rivers, which is confirmed by the co-occurrence with freshwater forms of the genera *Brotia* and *Sulcospira*.

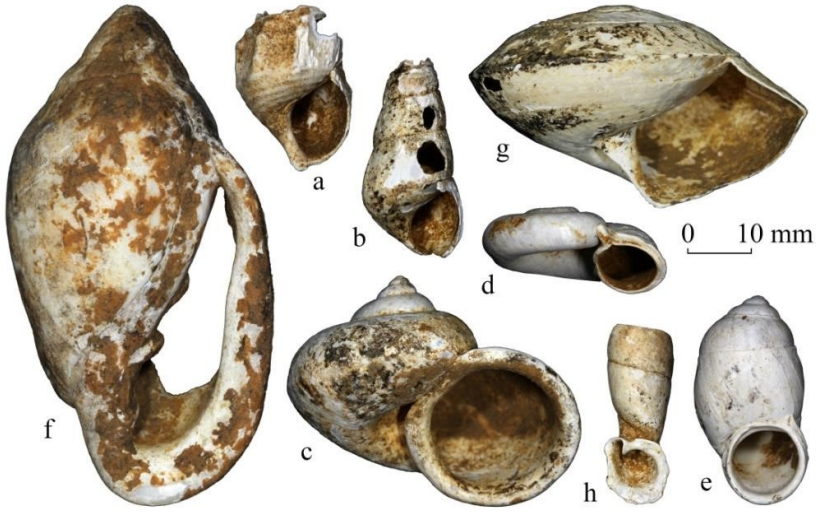

Fig. 2. Gastropods from the Lang Trang locality (all shells are figured from the aperture): (a) *Brotia jullieni* (Deshayes, 1874), specimen PIN, no. 5792/201; (b) *Sulcospira* cf. *collyra* Köhler et al., 2009, specimen PIN, no. 5792/202; (c) *Cyclophorus fasciatus* Kobelt, 1908, specimen PIN, no. 5792/203; (d) *Rhiostoma morleti* (Dautzenberg et Fischer, 1906), specimen PIN, no. 5792/204; (e) *Pollicaria rochebruni* (Mabille, 1887), specimen PIN, no. 5792/205; (f) *Ellobium aurismidae* (Linnaeus, 1758), specimen PIN, no. 5792/206; (g) *Camaena vanbuensis* Smith, 1896, specimen PIN, no. 5792/207; (h) *Megalauchenia proctostoma* (Mabille, 1889), specimen PIN, no. 5792/208; Vietnam, Thanh Hoa Province, Ba Thuoc District, Lang Trang cave; lower Upper Pleistocene.

4. CONCLUSIONS

The environments of the Lang Trang fauna are characterized by mosaic biotopes with a predominance of wet habitats with mangrove swamps and coastal lowlands. Such conditions could have existed in the area of the cave during the major marine transgression during the beginning of the Late Pleistocene.

In terms of age and taxonomic composition of the mammal assemblage (in particular, due to a simultaneous presence of three species of rhinoceroses, i.e. *Dicerorhinus sumatrensis, Rhinoceros sondaicus*, and *R. unicornis*), the Lang Trang fauna is similar to the fauna of the Coc Muoi locality in the Lang Son Province, northeastern Vietnam (MIS6-5, 148-117 ka BP). The ecosystems of the northern part of the Indochina Peninsula (23-20º N) during this time are characterized by the abundance and diversity of megaherbivores mammals. These ecosystems experienced a strong stress associated with the destabilization and changes of climate (including an increase in the intensity of the East Asian summer monsoon, which led to a general warming and humidification along with an increase in seasonal differences in precipitation) at the Middle and Late Pleistocene transition, and do not have modern equivalents.

Acknowledgements*: The study was carried out as part of work programme of the Joint Vietnam - Russia Tropical Science and Technology Research Center for 2020-2022 (Project E-1.4 "The Composition of the Fauna of Primates (Cercopithecidae, Pongidae) and Rodents (Rodentia) of the Pleistocene and Holocene of Vietnam as an Indicator of Environmental Change"). The authors are grateful to N.V. Serdyuk and A.A. Lozovsky (PIN), and I.V. Golovachev (Astrakhan State University) for fossil collecting in the Lang Trang cave in 2021, A.N. Kuznetsov and S.P. Kuznetsova (Tropical Center) for the assistance in expedition organization, S.V. Bagirov (PIN) for the help in illustration production. The local people of Canh Nang town and administration staff of the Ba Thuoc District, Thanh Hoa Province, helped the expedition.*

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SUMMARY

PLEISTOCENE LANG TRANG FAUNA IN NORTH VIETNAM: TAXONOMIC COMPOSITION AND HABITATS

New data on the taxonomic composition and ecological characteristics of Late Pleistocene vertebrates and invertebrates from the Lang Trang cave in northern Vietnam are presented. Based on the materials collected in progress of the work of the Joint Vietnam - Russia Tropical Science and Technology Research Center in 2020-2022, various representatives of the *Stegodon-Ailuropoda* Fauna of the second half of the Middle - early Late Pleistocene of Southeast Asia were identified,

including primates *Gigantopithecus blacki*, *Pongo* sp., *Trachypithecus* sp., *Presbytis* sp., *Macaca nemestrina*, *M.* cf. *fascicularis*, *M.* cf. *mulatta*, and *Macaca* sp., carnivorans *Panthera tigris*, *Neofelis nebulosa*, and *Arctonyx collaris rostratus*, a lipotyphlan *Chodsigoa hoffmanni*, a bat *Ia io*, rodents *Hystrix kiangsenensis*, *Leopoldamys neilli*, and *Rattus rattus*, proboscideans *Stegodon* sp. and *Elephas maximus*, perissodactyls *Tapirus indicus*, *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*, and *Rh. unicornis*, artiodactyls *Sus scrofa*, *S. barbatus*, *Tragulus kanchil*, *Hydropotes inermis*, *Muntiacus muntjak*, *Axis porcinus*, *Rusa unicolor*, *Capricornis sumatraensis*, *Bubalus arnee*, and *Bos* sp., a crocodile *Crocodylus* sp., a turtle *Cuora* sp. and an abundant gastropod association, presented by six terrestrial forms, two freshwater species and a coastal-marine species *Ellobium aurismidae*. *Gigantopithecus blacki*, *Macaca* cf. *fascicularis*, *M.* cf. *mulatta*, *Neofelis nebulosa*, *Chodsigoa hoffmanni*, *Ia io*, *Leopoldamys neilli, Rattus rattus*, *Rhinoceros unicornis*, *Sus barbatus*, *Tragulus kanchil, Hydropotes inermis*, *Axis porcinus*, crocodiles, turtles, and most of gastropod species were identified for the first time in the Lang Trang Fauna based on these studies. Of particular interest is the finding of the giant ape *G. blacki*, one of the latest in the fossil record. The habitats of the fauna are characterized as mosaic biotopes with a predominance of wet stations and the participation of mangrove swamps and coastal lowlands; these conditions could have existed in the area of the cave during a major marine transgression of the early Late Pleistocene.

Keywords: *Vietnam, Pleistocene, terrestrial vertebrates, gastropods, paleoecology.*

Nhận bài ngày 12 tháng 9 năm 2022
Phản biện xong ngày 10 tháng 11 năm 2022
Hoàn thiện ngày 23 tháng 8 năm 2023

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