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Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

The Late Pleistocene Duoi U'Oï cave in northern Vietnam: palaeontology, sedimentology, taphonomy and palaeoenvironments

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ARTICLE INFO

Article history:

Received 12 December 2007

Received in revised form

21 April 2008

Accepted 30 April 2008

ABSTRACT

This paper describes new fossil materials recovered at the Duoi U'Oï site, in December 2003, by a Vietnamese-French-Japanese team. The Duoi U'Oï cave is located in Man Duc village, 25 km of Hoà Binh city in northern Vietnam. It belongs to a karstic network developed in a dark grey micritic marine limestone dated from the Lower to the Middle Triassic.

The sedimentary fill produced a rich mammalian fauna, essentially composed of isolated teeth of middle- to large-sized mammals (Artiodactyla, Perissodactyla, Proboscidea, Carnivora, Rodentia, Primates), and characteristic of Late Pleistocene. The results of the Duoi U'Oï fieldwork are of great interest for the following reasons: (1) the biochronological age of the fauna is consistent with $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$ dating from the calcitic floors (66 ± 3 ka). The Duoi U'Oï fauna is thus the oldest well-dated modern fauna known for the Southeast Asian mainland; (2) in terms of sedimentology, the analysis of the formation of the fossiliferous breccia and that of the processes of deposits shows a close relation between the karstic deposits inside the cave and the deposits in the alluvial terraces. The observation of three levels of alluvial terraces associated with three caves situated at 62, 10 and 3 m above the present alluvial plain suggests that exokarstic and endokarstic sediments evolved together; (3) in terms of palaeobiogeography, Duoi U'Oï is the continental fauna showing the strongest resemblance with the Late Pleistocene faunas from Indonesian islands (Punung, Gunung Dawung, Lida Ajer, Sibrambang and Djambu caves); this implies that, at the time of Duoi U'Oï, ca 70 ka, the Sundaland was mainly characterised by faunas of modern aspect; (4) the analysis of major taphonomic factors that led to the mammal assemblage reveals a combination of selective agents (selective role of predators and porcupines, selective destruction of age classes for some species, selective preservation of fossils due to the deposition processes in the karstic network), which contribute to the poor representation of the diversity of the fauna; no arguments show that humans, present at Duoi U'Oï, might have a possible role in the taphonomic process; (5) the palaeoenvironmental reconstruction based on the composition of the faunal assemblage suggests a forested area and some open habitats, under warm and humid conditions.

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1. Introduction

In December 2003, the Duoi U'Oï site in northern Vietnam produced a rich mammalian fauna characteristic of the Late Pleistocene. This campaign was the third field expedition undertaken in the Hoà Binh Province by the Vietnamese-French-Japanese team (Roussé et al., 2003; Bacon et al., 2004, 2006; Demeter et al., 2004, 2005). The objective of this fieldwork was to

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gather information on the evolution and migration of the first Humans in continental Southeast Asia, *Homo erectus* and later *Homo sapiens*, in relation to patterns of mammalian dispersal.

During the last decade, certain scientific events dramatically called into question the widespread view concerning the evolutionary history of *H. sapiens* and *H. erectus* in this area. Swisher et al. (1994, 1996) and Swisher (1997), on the basis of new radioisotopic datings, have reconsidered the longevity of *H. erectus* in Java, and suggested a possible co-existence with *H. sapiens* up to the end of the Late Pleistocene (27 ± 2 to 53 ± 4 ka for Ngandong and Sambungmacan, datings contested by Grün and Thorne (1997) and van den Bergh (1999)). The discovery of a new hominid in Flores of around 18 ka, *Homo floresiensis*, has also strongly affected our knowledge of human evolution (Brown et al., 2004; Morwood et al., 2004, 2005). Indeed, this hominid, which presents morphological characteristics of endemic dwarfing, suggests for the first time an adaptation to insular conditions as occurs for any other very large mammals. This discovery also illustrates that *H. sapiens* was not the only hominid present in this area, and that the place of humans in Southeast Asian faunal associations and dispersals is still poorly documented.

The arrival of *H. sapiens* in the Sundaland, thanks to a sea level drop, in the first part of Late Pleistocene is accepted, but the precise moment of this event stays difficult to date. Modern Humans would enter this area with a stock of modern mammals like that which composes—but not totally—the Lang Trang fauna in Vietnam (de Vos and Long, 1993; Long et al., 1996). Several Indonesian sites, Punung (ca 80 ka) and Gunung Dawung in Java and Sibrambang, Lida Ajer (ca 80 ka) and Djambu (70–60 ka) caves in Sumatra, show this faunal turnover with the replacement of archaic mammals adapted to an opened habitat (like those of Ngandong) by modern mammals adapted to a lowland tropical habitat (Von Koenigswald, 1939, 1940; Hooijer, 1948; Badoux, 1959; de Vos, 1983, 1984, 1985, 1995; Leinders et al., 1985; Tougaard, 1998; van den Bergh, 1999; Storm, 2001; Storm et al., 2005; Bouteaux, 2005). Punung yielded a human tooth re-assigned to *H. sapiens* (Storm et al., 2005), but this assignment is not approved and thus cannot support the hypothesis that *Homo sapiens* reached the Sundaland with a migration of modern mammals so early (the new dating of 120 ka proposed by the authors being also questioned). The two human teeth from Lida Ajer are not more convincing (Hooijer, 1948; de Vos, 1983). For the moment, the only evidence for the presence of *H. sapiens* in this area in association with a modern fauna is the anatomically modern “deep skull” from Niah cave in the Kalimantan, dated around 50 ka (Gilbertson et al., 2005), or around 45–39 cal. ka (Barker et al., 2007 and all references therein about Harrison excavations).

In this context, the exploitation of the Duoi U’Oi cave provides some information: (1) in comparison with the nearby cave of Ma U’Oi in which the process of deposition is highly complex, resulting from multi-episode phases in the karstic system (Roussé et al., 2003; Bacon et al., 2004, 2006), in the cave of Duoi U’Oi, the depositional process seems simple and continuous; (2) the fossiliferous breccia yielded a fauna essentially composed of middle-sized to large mammals whose Late Pleistocene biochronological age is consistent with U/Th datings. It appears to be the oldest dated fauna of modern composition known at the present time for the mainland area; (3) its strong resemblance to Late Pleistocene modern faunas from Java and Sumatra enables the comparison of their species diversity and palaeoecology, and (4) the composition of the fauna with, among the large mammals (especially rhino), a high proportion of juveniles, and the state of preservation of teeth mainly gnawed by porcupines, enables the study of the taphonomy and the depositional processes.

2. Description of the Duoi U’Oi cave

2.1. Location and geological context

The Duoi U’Oi cave (coordinates: N20°37’12”, E105°16’25”) is located in Man Duc village (Tan Lac District, Hoà Binh Province, Vietnam), about 85 km SW of Hanoi, and 25 km SSW of Hoà Binh city (Fig. 1).

This area belongs to the northeastern extremity of the Annamitic Mountains chain and the western border of the Red River fault zone (Deprat et al., 1963; Luong, 1978a,b; Ky et al., 2001; Zuchiewicz et al., 2004). The NW–SE main folding axes in northern Vietnam are old tectonic structures that have probably existed since the early Carboniferous (Du Bois, 1985).

The landscape of Tan Lac District is characterized by a typical and spectacular morphology of karst peaks overhanging a mainly argillaceous alluvial plain level (Fig. 2). The so-called “tower-karst” or “inselberg” morphology developed in monotonous Carboniferous and Triassic limestone beds several hundred metres thick (Luong, 1978a,b; Deprat et al., 1963). On the Duoi U’Oi site, the bedrock consists of poorly fossiliferous dark grey micritic marine limestone dated from the Lower to the Middle Triassic (Luong, 1978a,b; Martini et al., 1998). On the whole, this Triassic basement is weakly folded with a dip rarely exceeding 15°/20°. The karstic limestone units show severe fracturing due to tectonic deformation. A dense network of caves, galleries and fissures developed in this framework partially driven by faults and fractures (Figs. 2 and 3) (Fenart et al., 1999).

In the neighbourhood of Man Duc village (Luong, 1978a,b), several caves expose sections of great interest for understanding karstic networks and their fill (Fig. 3). The caves are partly filled (less than 5% of cave volume on average) with brown to red-brown argillaceous and breccias material with numerous iron oxides pisoliths, bones and teeth. About 30% of the caves in the Man Duc area have this type of sedimentary fill (mainly Pleistocene and Holocene) and more than a half are fossil-rich even if this fill is often poorly preserved. Frequently eroded by recent water circulation, the Pleistocene karstic deposits often occur as residual material on the walls of the caves.

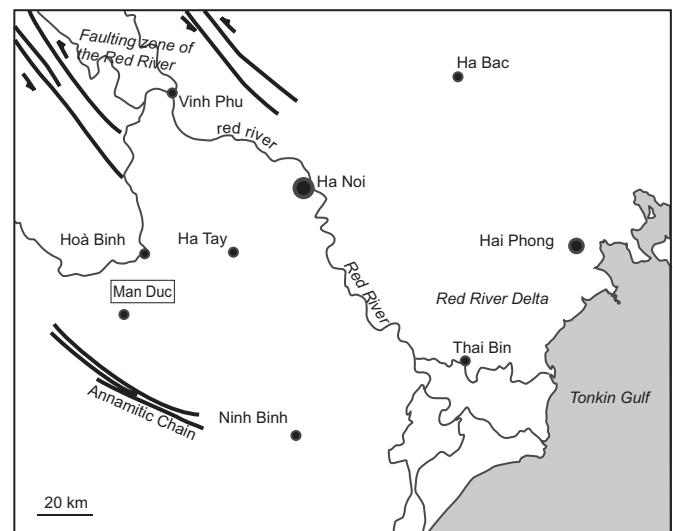


Fig. 1. Map of North Vietnam with the location of the studied area in the Annamitic Chain on the right border of the Red River delta. The cave is situated in Triassic limestone in the Tan Lac District (Hoà Binh Province), around 85 km SW from Hanoi, 25 km SSW from Hoà Binh city.

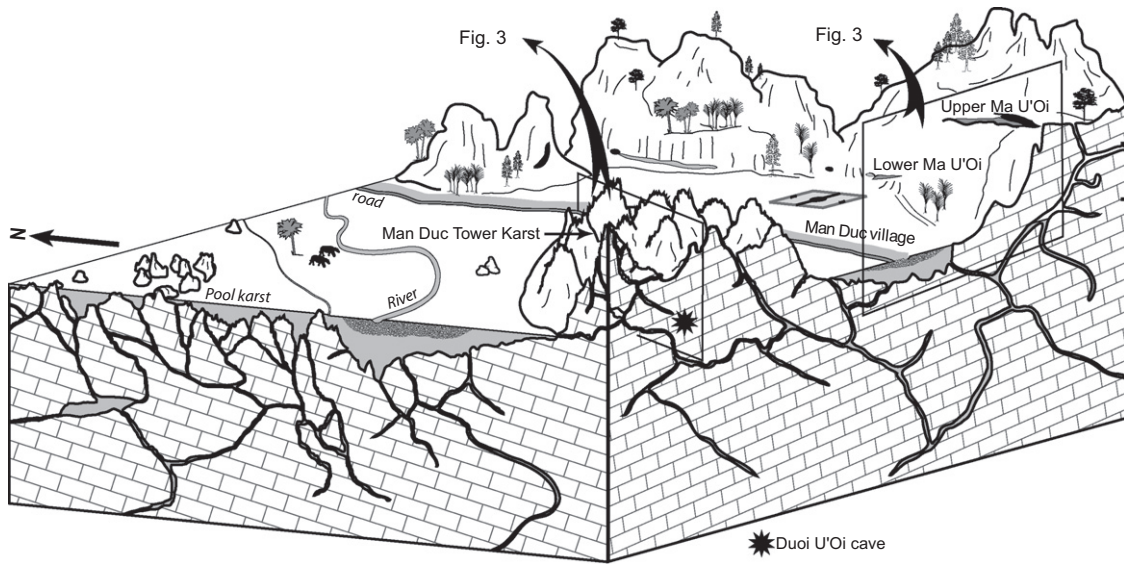


Fig. 2. Synthetic sketch of the “tower karst” morphology of the Man Duc site with the location of the caves (Upper and lower Ma U’O’i studied in previous works by Bacon et al. (2006), and Duoi U’O’i presented here). Duoi U’O’i is situated in the central tower karst just behind the houses of the village.

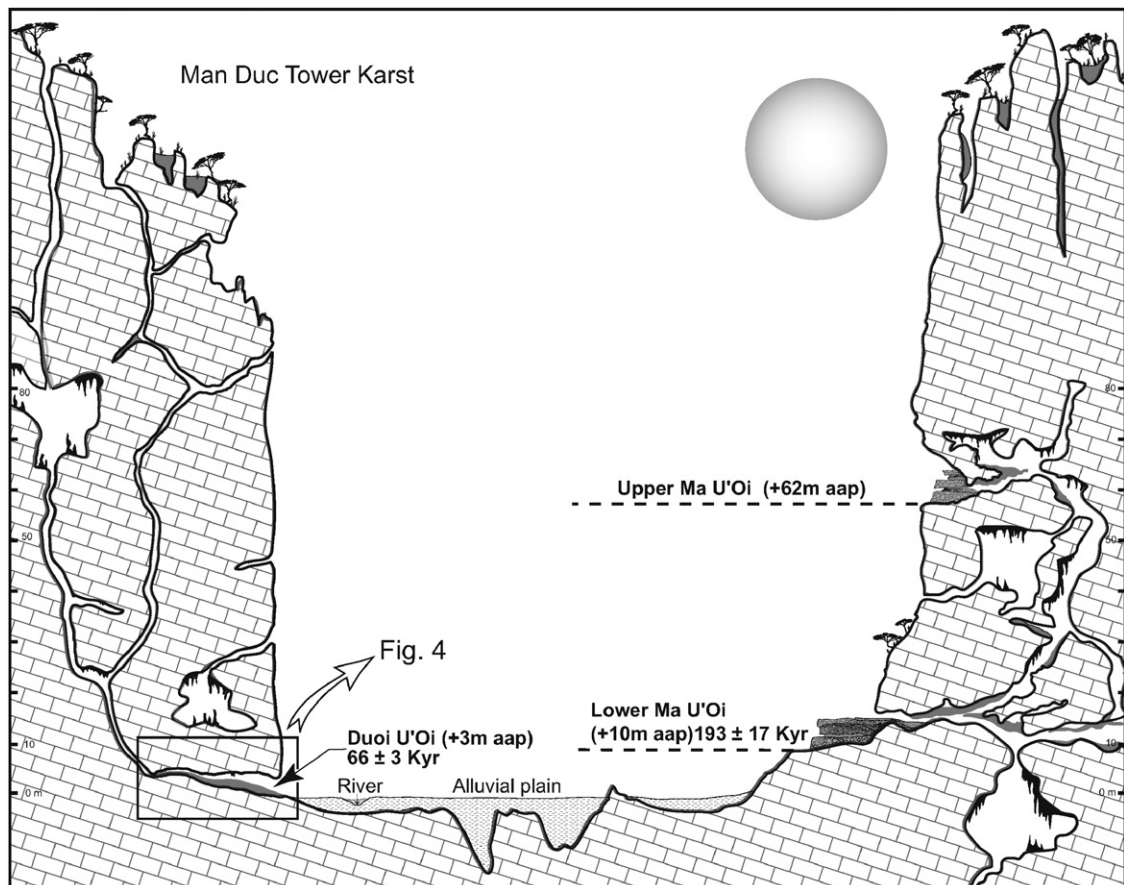


Fig. 3. Detailed sketch showing the precise level of the Duoi U’O’i cave, and those of the upper and lower Ma U’O’i caves. The dating of the caves indicates that the oldest caves are situated at the upper part of the cliff, and the youngest ones at the base. Each cave is linked to an alluvial plain level. During the time, the fall of the alluvial plain, directly linked to the combined variations of the tectonic uplift and sea level oscillations, enables the formation of new cavities and the opening of plugged ones in the lower part of the section. In this region, the Duoi U’O’i cave appears to be the youngest episode for the karst activities (opening/filling).

2.2. Plan of the cave

The Duoi U’O’i cave has been exploited because of its exceptionally well-preserved and uneroded Pleistocene fossiliferous breccia.

The entrance of the cave is located behind private houses, 3 m above the present alluvial plain (Fig. 3). The cave consists of two distinct corridors (corridors 1 and 2), which are connected together in a single corridor (corridor 3) 18 m away from the entrance (Fig. 4a). The diameter of corridor 3 decreases rapidly at

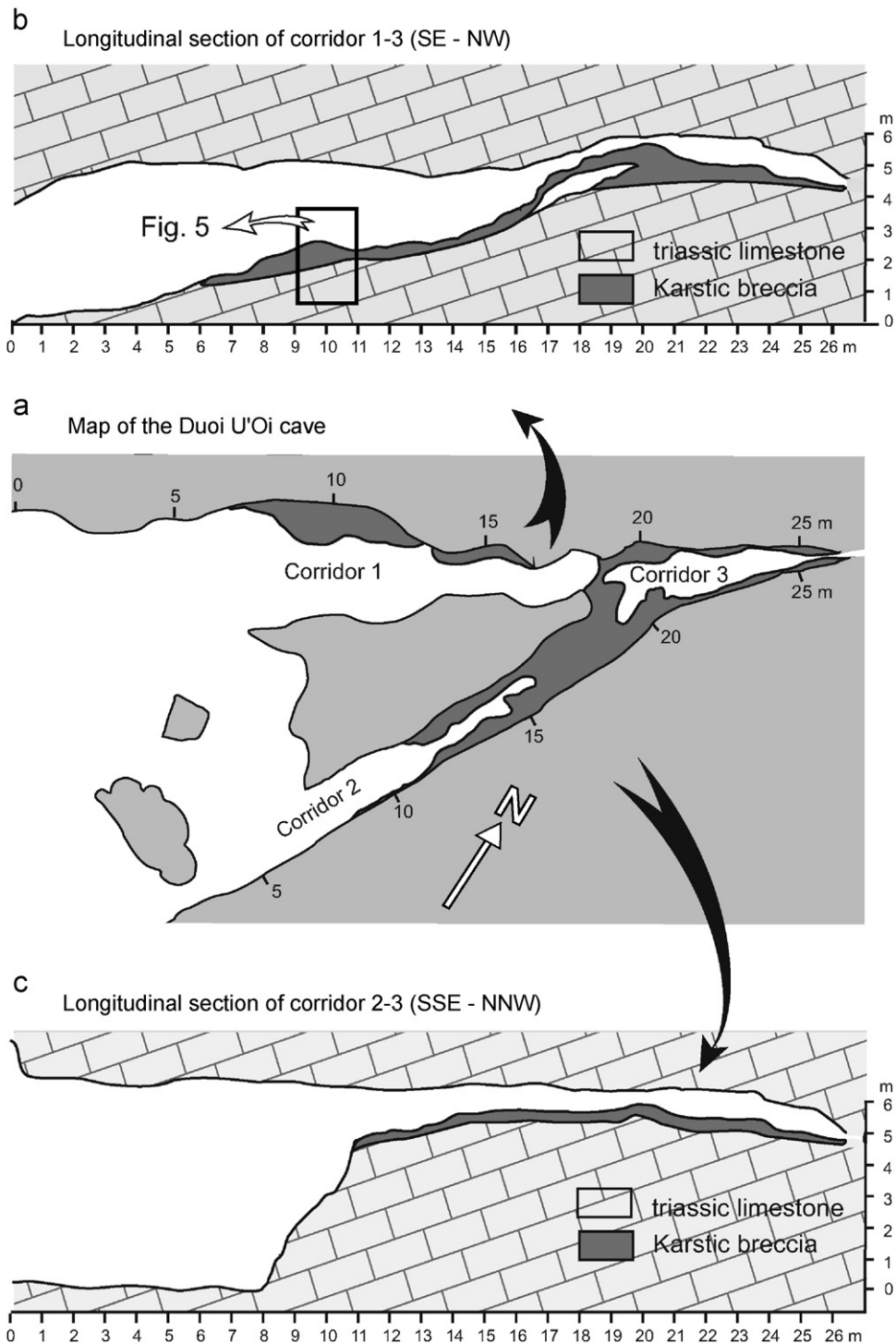


Fig. 4. Map (a) and vertical sections (b and c) of the Duoi U'O'i cave. Corridors 1 and 2 are largely open on the present alluvial plain. The Pleistocene breccia is well developed in corridor 1. Corridors 1 and 2 are connected together in a single corridor (corridor 3) 18 m from the entrance. Corridor 3 is partially a dead end. Only the lower part and upper part of corridor 1 were exploited during this fieldwork.

26 m, and farther on only a small hole around 40 cm in diameter exists (Fig. 4b and c).

During the fieldwork, we mainly excavated corridor 1 and especially its lower part close to the entrance (Fig. 4a and b) for three main reasons: 1—the fossiliferous breccia is particularly well developed and is almost 1 m thick (for 0.4 m and even less in other places in the cave); 2—the breccia is highly fossiliferous in

the lower part; and 3—the sedimentary fill of corridor 1 appears to be less cemented by calcite encrustation than in corridor 2 and the base of the section is clays-rich, making the excavation easier. For the same reasons we also excavated the end of corridor 3 (between 23 and 26 m). The breccia of corridor 2 was not excavated. It was particularly poor in fossils and very strongly cemented by calcite.

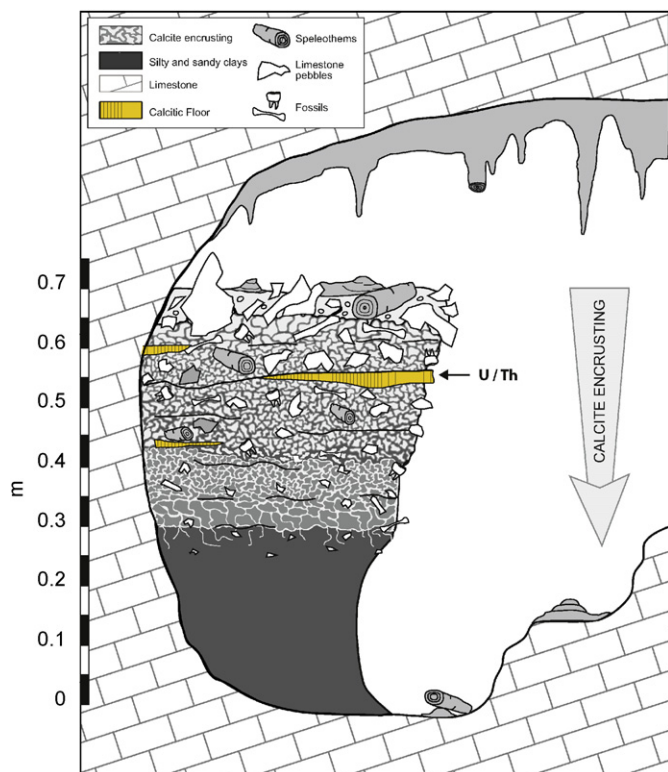


Fig. 5. Stratigraphic section of the lower part of the cave fill, which shows two distinct units: the lower unit formed by sandy clays is overlaid with strongly encrusted breccias. The largest clasts are situated at the upper part of the section in a coarsening-up sequence. The clasts are mainly formed by Triassic angular to poorly rounded limestones, and reworked speleothemes. Inside the breccia, one of the developed calcitic flowstone, chosen among 2 or 3 samples, has been used to dating (U/Th).

3. Analysis of the sedimentary fill

3.1. Description of the sedimentary fill

The sedimentary fill consists of the superimposition of two distinct layers: an argillaceous silty-clay at the base and a pisolite-rich fossiliferous muddy calcareous breccia above (Fig. 5). The brown-red basal silty to sandy clay is well developed in the lower parts of corridor 1 and at the end of corridor 3 (Fig. 4). Sandy clays are totally absent in corridor 2. The basal silty to sandy clays contain a lot of mammal teeth, and numerous weathered and coloured shells of snails (terrestrial pulmonates gastropods close to *Ryssota* or *Acavus*). The breccia at the top of the section is characterised by very angular to poorly round Triassic limestone pebbles, many speleothems (reworked stalactite and calcitic encrustations) and many teeth. The same shells described in lower argillaceous layers occur here as broken pieces. Some more or less discontinuous *in situ* calcitic layers occur at several levels inside the breccia (Fig. 5). Because of the high weathering of the breccia and the lack of clear sedimentary structures, the analysis of the fill of the cave is very difficult. The informations are given both by the reverse gradient from the base to the top and by the disposition of the clasts on the upper part of the section.

The breccia (Fig. 5) is composed of a sequence that is increasingly coarse, both from the base to the top of the section and from the entrance to the end of the cave (mainly in the lower part of corridor 1, from 7 to 17 m, Fig. 4). In fact, the greatest volume of breccia is concentrated exactly just before the place where the corridor is strongly funnel-shaped (between 8 and 14 m

in the corridor 1, Fig. 4a and b). After 17 m and towards the back of the cave, the average diameter of the cavern, as well as the thickness of the sedimentary fill, is strongly reduced. In the upper part of corridor 1 (17–19 m) and in corridors 2 and 3, the coarse-grained sedimentary fill is essentially arenitic with numerous iron oxide pisolites. Coarse-grained material or small pebbles are totally lacking in the upper parts of corridors 1 and 3. Bones and teeth are rare in corridor 2 whereas they are abundant in the upper part of corridor 3. In the lower section of corridor 1, the largest clasts are concentrated at the top of the breccia, many of them (especially the most flattened ones) being imbricated obviously downwards in the cave. Some of them can reach up to 30–40 cm in diameter.

The upper part of the sedimentary fill in the Duoi U'O'i cave is entirely encrusted with calcite that diffuses downwards to layers that are sometimes argillaceous (Fig. 5). The intensity of calcite encrustation decreases progressively from the top to the base of the section. The upper part of the stratigraphic column (0.3–0.7 m) is characterized by several small (centimetre scale) discontinuous calcitic floors, showing that the sedimentary material deposited in several phases is separated by small calcite encrustations.

3.2. Interpretation and sequence of the sedimentary processes

The Duoi U'O'i cave deposits (sandy clays and breccia) are similar to those observed in the neighbourhood, at Ma U'O'i cave (Roussé et al., 2003; Bacon et al., 2004, 2006; Demeter et al., 2005), but they are much easier to interpret. The argillaceous deposits at the base and the breccia in the upper part of the section appear to be superimposed without major erosion, as it is the case at different levels in the Ma U'O'i cave (remains of breccia appear as relics on the walls of the cave).

The presence of a well-developed unit of silty to sandy clays at the base of the cave as well as a lack of pebbles or coarse-grained sediments suggest a very low water circulation inside the karst before the breccia deposit (Fig. 6a). The concentration of molluscs in the basal clay seems to be linked to their buoyancy capacity (frequent occurrence of air inside the shell). The sedimentation of such a thick unit of fine argillaceous material strongly suggests that the cave was flooded, or had at least a highly reduced water circulation after the filling of holes with water, which would permit the slow decantation of such thick pelitic material. The cave was undoubtedly situated beneath the water base level (i.e. under the alluvial plain) (Fig. 6a).

The excellent imbrication of flattened angular clasts (oriented downwards), the great abundance of reworked speleothems (stalactites, calcitic floors) as well as the lack of alluvial sediments (fluvial pebbles for example) are evidence for a water circulation from the inside to the outside of the cave. In addition, the fact that no clasts (pebbles or bones) larger than the corridor diameter at the upper part of the cave have been found corroborates this hypothesis. Limestone clasts, Fe–Mn-rich pisoliths, arenitic material as well as bones and teeth were thus all transported inside the karst by powerful water flows from the top of the inselberg (at that time, the limestone massif was not yet dissected into small inselbergs). The general increased coarsening in the sequence of the section shows that strong water flows were responsible for erosion and deposits that gradually increased over time.

The occurrence of numerous flattened small erosion surfaces inside the breccia as well as thin calcitic floors, which were sometimes eroded, indicate that the deposits of the breccia clearly represent several phases of cave flooding separated by weak to intense calcite encrustation. Regarding the time necessary for the formation of centimetre-scale calcite floors in the breccia, the alternation of flood deposits and partly drying-up of the cave

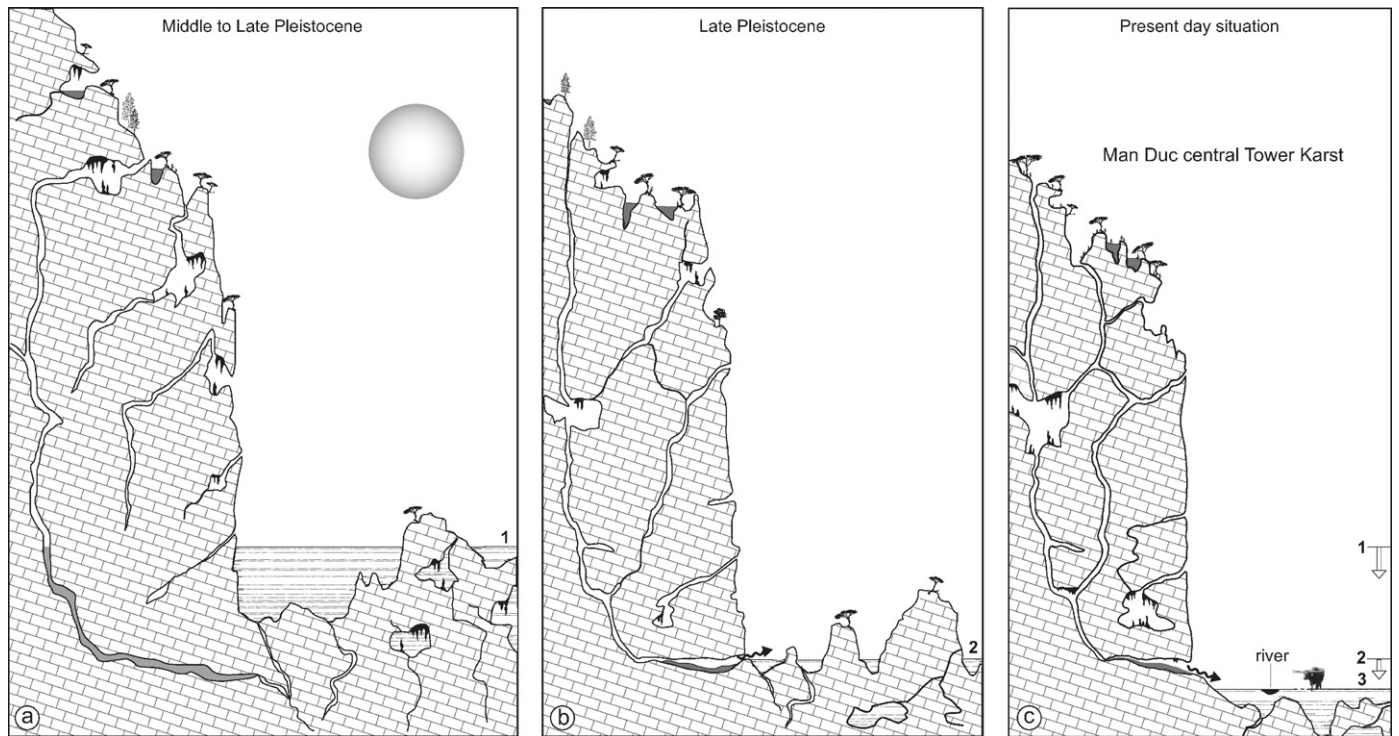


Fig. 6. Synthetic sketch showing the formation of the cave and the history of the fill. (a): the deposition of the silty to sandy clays at the base of the section suggests that the water circulation was reduced. Such conditions occur often in the caves which are situated under the alluvial plain level, and which are partially to entirely drowned. (b): the deposition of the breccia, characterised by a well-developed coarsening-up sequence, supposes an active water circulation and a progressive opening of the cave that enables transport of coarse-grained material. Between the water circulations phases (mainly flooding), the breccias are partly encrusted by calcites. (c): present-day situation. The breccias strongly encrusted by calcite sedimentary fill (breccias and silty to sandy clays) were partially reworked during flooding phases after a new fall of the alluvial plain level. The main sedimentary processes in the cave are calcite encrustation that occurred during dry phases, and erosion that occurred during flooding phases.

(calcite encrustation) suggests a fill that took place over at least several hundred or even a thousand years. The size increase of the clasts from the base to the top of the breccia could be related to climate change or to a gradual opening of the karstic network that permitted the circulation of heavier water flows. The transport of coarsened-grained arenites and conglomeratic material suggests that the cave could now be situated over the alluvial plain (Fig. 6b) (modern caves and karstic networks under the present alluvial plain in the neighbourhood are generally flooded and completely plugged by argillaceous sediments).

After the last breccia deposits, at the beginning of the complete drying-up of the karst, the top of the breccia is strongly encrusted with calcite and partly consolidated (Fig. 6c). In the lower part of the cave near the entrance, the partial to total erosion of the described section suggests a new fall in the base level (alluvial plain).

3.3. Dating of the calcitic floors by the $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$ method

A sample from the calcitic floors (flowstone) at the level 0.55 (Fig. 5) has been dated by using the classic $^{238}\text{U}/^{234}\text{U}/^{230}\text{Th}$ disequilibria method (see Edwards et al., 2003; Chabaux et al., 2003 for the theoretical aspects). The carbonate sample had the necessary requirements for obtaining reliable ages from the direct measurement of ^{238}U – ^{234}U and ^{230}Th – ^{234}U disequilibria without correction of the initial Th: its composition is of pure calcite, without evidence of recrystallisation and/or secondary carbonate deposit (e.g. Schwarcz and Blackwell, 1992). This was checked respectively by X-ray diffraction and careful thin section examination.

The determination of ^{238}U – ^{234}U and ^{230}Th – ^{234}U disequilibria in the calcitic floor sample requires the determination of the U/Th content ratio and the U and Th isotopic compositions that were measured at the “Centre de Géochimie de la Surface” (Strasbourg,

Table 1

U-series data and calculated ages for the flowstone samples. ($^{234}\text{U}/^{238}\text{U}$) is the initial ratio at the time of deposit

[U] (ppm)	[Th] (ppm)	($^{234}\text{U}/^{238}\text{U}$)	($^{230}\text{Th}/^{234}\text{U}$)	Age (ka)	($^{234}\text{U}/^{238}\text{U}$) _i
0.70 ± 0.01	0.0084 ± 0.0002	1.082 ± 0.005	0.460 ± 0.01	66 ± 3	1.099 ± 0.007

France). About 3 g of finely crushed or ground carbonate were dissolved in dilute acid (1 N HNO₃). After drying, the solution was dissolved again in 7.5 N HNO₃ acid. An aliquot, corresponding to around 100 mg of the sample, was used for U and Th concentration determinations by isotope dilution with a mixed $^{235}\text{U}/^{230}\text{Th}$ spike. The U and Th isotope measurements required for this determination were performed on a VG-54 sector mass spectrometer. The remaining solution was used for analysing $^{234}\text{U}/^{238}\text{U}$ and $^{230}\text{Th}/^{232}\text{Th}$ ratios by Thermal Ionisation Mass spectrometry on a thermo-Finnigan Triton. Details of the U–Th TIMS analyses procedure can be found in Dequincey et al. (2002) and Granet et al. (2007). The chemical purification used for U and Th isotopes was slightly adapted from procedures ordinarily used at CGS (e.g. Rihs et al., 2000; Dequincey et al., 2002; Durand et al., 2005).

The U and Th contents and the isotope ratios of the sample are given in Table 1. The very low Th content (0.0084 ppm) confirms that this sample is nearly devoid of detrital contamination. From the ($^{234}\text{U}/^{238}\text{U}$) and ($^{230}\text{Th}/^{234}\text{U}$) activity ratios, the age of the sample can be calculated using the classic equation of Kaufman and Broecker (1965), stipulating that no initial ^{230}Th was present in the sample. The ISOPLOT code (Ludwig, 1994) used for the calculation of this age gives an age of 66 ± 3 ka. The age of the flowstone, covering the level from which the teeth were recovered, provides the upper limit of the absolute estimate.

3.4. Chronology of the Endokarstic and Exokarstic deposits

In the neighbourhood of the Duoi U'Oï site several networks of caves appear at different elevations above the fluvial plain (Figs. 2 and 3) (Bacon et al., 2006). At least three levels of alluvial terraces could be observed, situated at 62, 10 and 3 m above the present alluvial plain, in a stair-like disposition (respectively upper Ma U'Oï, lower Ma U'Oï and Duoi U'Oï) (Fig. 3). One important observation is that each alluvial terrace is more or less at the same elevation as the access to a cave. These alluvial sediments consist mostly of conglomeratic channel-stream deposits interstratified with sandy/silty alluvial plain or temporary pond deposits. In some places, they are interstratified with horizontal calcite layers, corresponding to exokarstic crystallisations (calcitic floors).

Several U/Th datings have been carried out on such flowstone from both upper and lower Ma U'Oï “terrace–cave couples” (Bacon et al., 2006) (Fig. 3). Because of argillaceous pollution, the upper Ma U'Oï calcitic floor provided no data. However, one sample from lower Ma U'Oï (from the breccia that contains microvertebrates) revealed an age of 193 ± 17 ka (Bacon et al., 2006) (i.e. late Middle Pleistocene). The new dating from Duoi U'Oï gives an estimation of 66 ± 3 ka.

The close relation between the karstic deposits inside the caves and the deposits in the alluvial terraces is evidence that these endokarstic and exokarstic sediments evolved together. Thus, each terrace corresponds to an old alluvial plain, which gradually lowered over time, the exit of the galleries being readjusted automatically to the new position of the alluvial plain. The stair-like geometry of the terraces, associated with cave formation (“terrace–cave couple”), indicates at least three successive lowerings of the Quaternary alluvial plain: upper Ma U'Oï (62 m above the current plain), lower Ma U'Oï (10 m) and Duoi U'Oï (3 m). The present-day alluvial plain level corresponds to the last drop since the Duoi U'Oï fill. According to the datings of Ma U'Oï and Duoi U'Oï, the lowering of the alluvial plain could be about 1 m every 20,000 years (18,000 years between lower Ma U'Oï and Duoi U'Oï, and 22,000 between the latter and the present alluvial plain).

There is simultaneous fill of the cave and an accumulation on the alluvial plain, both related to the relative position of the base level. When the base level dropped due to regional tectonic movements and/or eustatic oscillations, the fill in the caves was partly eroded and occurs as relicts on walls in the karstic network (see the example of Ma U'Oï cave in Bacon et al., 2006). In the same way, the stair-like profiles of the palaeoterraces formed gradually with the lowering of the valley. These variations recorded in the karstic fills may be associated with variations in rising and erosion rates or global climatic oscillations during the Pleistocene.

In surrounding areas (Dien Bien Phu basin, W/NW of the studied area), a recent tectonic activity was observed (Zuchiewicz et al., 2004) on the basis of a description of perched alluvial deposits, with a dating range from the Late Pleistocene to the Holocene. The combination of sea level oscillations with an active tectonic background could be the most relevant factor for explaining the structure of the depositional units (stair geometry). Moreover, the distance of the Man Duc site from the Red River delta plain (less than 30 km) suggests that the Pleistocene sea level oscillations controlled the base level and subsequently the karstic and alluvial dynamics.

The high-resolution sea level pattern proposed by Molodkos and Bolikhovskaya (2002) for the last 600 ka, in northern Eurasia, suggests a correlation between sea level and the development of sedimentary fill. The period of fill of the Duoi U'Oï cave as well as that of Ma U'Oï corresponds to a phase of a major drop in sea level (between 120–20 and 215–140 ka, respectively).

4. Analysis of data

4.1. Palynology

4.1.1. Methodology

Palynological samples (M1 to M8 from segments 10–11 and 24 in the corridors of the cave) were taken in the field by Nguyen Thi Mai Huong, and were then prepared and analysed at the laboratory of palynology (CEPAM-CNRS/UNSA Nice) (Table 2, Fig. 4). The samples were prepared with a classic physico-chemical treatment, followed by a heavy liquid levigation (Girard and Renault-Miskovsky 1969), and also a direct levigation according to a method employed at the laboratory of Marseille (Goeury and de Beaulieu, 1979). Both methods were used in order to be very appropriate, because of the poor palynological content of the Duoi U'Oï deposits.

The first method uses hydrochloric and hydrofluoric acids successively to eliminate carbonates and silicates. A treatment with potash was used in order to render humates soluble. However, much more insoluble material often remains (solution) in which we could find pollen grains. This is the reason why we separate them by flotation in a solution of density 2. Lighter pollen reassembles in the floating sediment, while dense minerals fall down to the bottom of the tube. This solution is then filtered with a filter of calcium carbonate. The destruction of this filter by hydrochloric acid enables the pollen grains to be collected, and then isolated from the residual gangue. Later, the pollen is coloured by fuchsine.

The second method consists of placing the sediment in suspension in a heavy liquid (Thoulet's solution). The floating sediment is then filtered with a cellulose filter, which is destroyed by acetylosis treatment. Residual minerals are eliminated by the action of hydrochloric and hydrofluoric acids. The pollen became yellow because of the acetylosis treatment but was not coloured further.

4.1.2. Results

Despite the use of these two advance methods, few pollen grains were found during observation with a microscope. They are rare and altered and the list is poor (Table 2). The conditions of sedimentation (fast or not), the physico-chemical nature of the soil (rich or not in alkalis), the climatic conditions (with alternation of dryness and wetness for example), alone or combined, are factors that are probably responsible for this poor preservation of palynological elements. It should be more appropriate in the future to take samples in more remote parts of the cave, where the karstic area is more stable and independent from exterior climatic conditions (with constant humidity, temperature, etc.).

Table 2

Results of the palynological analyses of the eight samples from the sediments of the cave (segment 10–11, except the sample M7 from the segment 24)

Samples	Segments	Type of pollen grains
M1	10–11	2 Poaceae, 2 Polypodiaceae, 4 Indet.
M2	10–11	2 <i>Pinus</i> , 1 t. <i>Rhizophora</i> , 6 Poaceae, 2 Polypodiaceae, 2 <i>Selaginella</i> , 6 Indet.
M3	10–11	3 Poaceae.
M4	10–11	1 Poaceae, 1 Polypodiaceae, 1 Betulaceae, 1 Indet.
M5	10–11	1 Poaceae, 1 Indet.
M6	10–11	1 <i>Pinus</i> , 1 Polypodiaceae, 2 Indet.
M7	24	6 Poaceae, 2 Polypodiaceae, 4 Monolet fern spores without perisporium, 6 Indet.
M8	10–11	1 <i>Pinus</i> , 1 Fabaceae, 1 Polypodiaceae, 1 <i>Microlepia</i> , 2 Indet.

Indet: undetermined taxon. See Fig. 4 for the location of segments in the cave.

4.2. Palaeontology

4.2.1. Methodology

The Duoi U'O'i faunal remains consist essentially of mammalian teeth. These teeth come from two loci inside the cave (Fig. 4a and b): the segment 10–16 in the corridor 1 (920 isolated teeth), and the segment 23–25 in the corridor 3 (269 teeth). The fossiliferous breccia has been extracted using a pneumatic hammer, and crushed in small fragments. All the sediments were then screened with a sieve of 3 mm. Despite this systematic sieving, no microvertebrates have been found.

The teeth coming from the two loci (segments 10–16 and 23–25) do not present significant differences in morphology and size, which suggests that they could represent two faunas of different ages, resulting from two deposits separate in time. Only some *in situ* teeth from the segment 23–25 found close to the surface of the soil display a different patina with traces of recent fire activities.

4.2.2. Description

All the determined materials of Duoi U'O'i are listed in Table 3. It is compared with that of other principal Pleistocene sites from South China, Thailand, Cambodia, Vietnam, Laos and Indonesia (Fig. 7).

4.2.3. Artiodactyla

The Artiodactyla recorded are cervids, bovids and suids. Some elements are figured in Fig. 8. The dimensions of the teeth are presented in Table 4.

4.2.3.1. Cervids. The Duoi U'O'i fauna includes two cervids (Table 3): one of large size whose teeth conform to *Cervus unicolor* Kerr, 1792, and the other of small size attributable to *Muntiacus muntjak* (Zimmermann, 1780).

The large cervid is known through numerous isolated teeth, most of which present gnawed roots. In the record are 88 permanent and 11 deciduous teeth assigned to *Cervus unicolor* (or *C. cf. unicolor* when worn or fragmentary). Concerning the permanent upper teeth, the premolars present the standard characteristics of this species: some that have been determined as P2 or P3 have two distinct lobes on the lingual side with a clear separation between the voluminous protocone and hypocone, a well-marked metastyle and a small parastyle. Others have only a small groove between the two lingual cusps, with metastyles variably salient. The upper molars have developed bilobate even trilobate entostyles, a voluminous hypocone, a spur sometimes present on the posterior lobe, well-developed styles and pillars, an anterior well-developed notched goat fold, and also numerous foldings of the cingulum on the overall crown. Some lower premolars are not molarised like p2 or p3 of the modern species. Some others display an advanced molarisation, sometimes complete with the presence of a lingual wall (Fig. 8). Heintz (1970) described in detail the different degrees of molarisation that concern some Villafranchian cervids. In comparison, the large Duoi U'O'i cervid presents a high degree of molarisation with the closure of the second valley (between metaconid and paraconid). The metaconid is mesiodistally elongated with anterior and posterior wings, the anterior wing uniting with the paraconid. On some teeth can be observed the closure of the fourth valley (between entoconid and entostylid), the bending of the protoconid and the oblique orientation of the entoconid. Lower m1 and m2 have an anterior goat fold, with a notched cingulum, and the bilobate ectostylid is always present. On the buccal surface there are sometimes small pillars between the cusps. The m3 have the same characteristics: a well-marked anterior goat fold, notched enamel in the outline of the crown, and pillars on the buccal surface. A second pillar is frequently present between the hypoconid and hypoconulid.

The upper and lower molars (Table 4) conform to the size variability of other fossil specimens from Lang Trang (de Vos and Long, 1993). The size of the molars of *Axis porcinus* and *Cervus eldii* are comparatively smaller overall. The premolars of Duoi U'O'i are larger than those of comparative samples. The dimensions of P3 and P4 exceed the known ranges of recent and fossil *C. unicolor* (Thum Wiman Nakin; Tougard, 1998), on small samples.

The data set of the Duoi U'O'i *C. unicolor* also includes deciduous teeth. Two D3 conform to the pattern of modern *C. unicolor* with well-developed styles, a pillar of paracone more salient than that of metacone, posterior wings more elongated than the anterior wings in the paracone as well in the metacone. The four available d4 have very salient stylids, especially the parastylids, mesostylids and metastylids. The three pillars of conids are developed in a similar way with symmetrical anterior and posterior wings. The columns are present on the buccal and lingual sides. Metric comparative data are either non-existent or too scarce to form a conclusion. Only the size of d4 exceeds that of Phnom Loang (Tin Thein, 1974).

The Duoi U'O'i cervids also include a small-sized muntjac. Many isolated teeth are worn or fragmentary, while others are attributable to *M. muntjak*. The complete sample is composed of 15 deciduous and 99 permanent teeth (Table 3).

Among the upper premolars, P2 can be easily distinguished from P3/P4. The voluminous protocone is separated from the hypocone by a deep groove and the metastyle is very salient accentuating the asymmetry of the tooth. It is more difficult to distinguish P3 from P4, these features being less pronounced. The protocone and the hypocone are equal in size with a less-marked groove (sometimes absent). The metacone is not developed, and the styles (metastyle and parastyle) tend towards a similar pattern. The upper molars are cone-shaped, the parastyle and mesostyle are strongly developed, ectostyles are present close to the hypocone, the pillar of the paracone is more marked than that of the metacone and the pillars of the protocone and the hypocone are oblique. On the lower premolars, the metaconid is inclined towards the distal part of the crown and the protoconid and hypoconid are separated by a shallow groove. The p3 have a fused paraconid and parastylid, both separated from the metaconid by a very deep groove. The lower molars have ectostylids of variable height on m1/m2/m3. We find on some m3 a second column between the hypoconid and the hypoconulid.

Dental size (Table 4) has a range within the modern and fossil specimens from Phnom Loang (Tin Thein, 1974), Thum Wiman Nakin (Tougaard, 1998) and Ma U'O'i (Bacon et al., 2004). The muntjac from Yenchinkuo *Muntiacus muntiacus margae* cannot be compared with that of Duoi U'O'i as the data presented are rows of teeth rather than isolated elements (Colbert and Hooijer, 1953). Only one tooth (DU460) largely exceeds the *Muntiacus* dimensions and does not match the *Cervus* data either.

Fifteen deciduous teeth are listed at Duoi U'O'i. The D3 have well-developed styles, especially the mesostyle. The pillars of paracone and metacone are marked. The lingual wall of the anterior lobe is very elongated. We question the presence of a protocone fold on one tooth (DU522). The D4 have few pronounced metastyles. Concerning these teeth, it is sometimes difficult to distinguish them from upper permanent molars, as some are small and highly worn. Even the height of the crown and the width of the enamel are not sufficient features to form a conclusion. The two d4 have a hypoconid that is as developed as other cusps. Two ectostylids are present. The dimensions of the deciduous teeth of the muntiacines from Duoi U'O'i are comparable to the modern sample.

4.2.3.2. Bovids. The proportion of bovids in the Duoi U'O'i fauna, in comparison to that of the cervids, is minor. Indeed, the breccia has

Table 3

Record of Duoi U'Oi materials for each taxon. Among the 1189 elements recovered, most are well-preserved teeth and are attributable to one species

Taxa	Upper permanent teeth	Lower permanent teeth	Upper decidual teeth	Lower decidual teeth
<i>Cervus unicolor</i>	1 P2, 1 P3, 6 P4 24 M	6 p2, 4 p3, 13 p4 15 m1/m2, 18 m3	4 D2, 2 D3, 1D4 –	4 d4 –
<i>Muntiacus muntjak</i>	12 P2, 19 P3, 7 P4 30 M	2 p2, 5 p3/p4 24 m	2 D3, 11 D4 –	2 d4 –
<i>Nemorhaedus sumatrensis</i>	4 M1/M2, 1 M3	1 m1/m2, 4 m3	–	–
<i>Bubalus cf. bubalis</i>	–	1 p, 1 m	–	–
<i>Sus scrofa</i>	31 P1 to P4 43 M1/M2/M3	29 p2 to p4 43 m1/m2/m3	2 D3, 2 D4 –	4 d2, 2 d4 –
<i>Sus barbatus</i>	3 M3	2 m2	–	–
<i>Rhinoceros unicornis</i>	–	1 p2, 4 p4 2 m1, 1 m2, 1 m3	–	1 d1, 6 d3 –
<i>Rhinoceros sondaicus</i>	–	2 p2, 2 p3 6 (1 m1, 1 m2, 4 m3)	5 D1 to D4 –	5 d3 –
<i>Rhinoceros sp.</i>	1 M1, 2 M3 –	–	1 D4 –	2 d3 –
<i>Dicerorhinus sumatrensis</i>	1 M (?)	–	–	–
<i>Rhinocerotina indet.</i>	1 M3	1 m2, 1 m3	–	–
	–	–	–	4 d4
	1 M2	1 m (?)	–	–
<i>Tapirus indicus</i>	1 P 4 M1/M2	1 p3 2 m2, 2 m3	1 D4 –	– –
<i>Elephas sp.</i>	4 M	3 m (2 m 1)	2 D2 (?), 1 D4	–
<i>Arctonyx collaris</i>	2 I3 2 P4 4 M1	– – 1 m	– – –	– – –
Melinae indet.	1 P4	–	–	–
<i>Cuon alpinus</i>	9 P1 to P4 1 M1	9 p1 to p4 2 m2	– –	– –
Carnivora indet.	1 M2	–	–	–
<i>Viverra zibetha</i>	1 P4 1 M1	– –	– –	– –
<i>Viverra cf. megaspila</i>	1 M1	–	–	–
Viverridae indet.	–	1 p	–	–
<i>Neofelis cf. nebulosa</i>	1 P4	–	–	–
<i>Panthera pardus</i>	–	3 p3, 3 p4 2 m1	– –	– –
<i>Panthera tigris</i>	–	1 m1	–	–
<i>Panthera sp. (i.e. tigris or pardus)</i>	4 C	2 c	–	–
<i>Ursus thibetanus</i>	4 I 5 C 3 P4 3 M1, 3 M2	– 3 c – 1 m2	– – – –	– – – –
<i>Helarctos malayanus</i>	–	2 m1	–	–
<i>Hystrix brachyura</i>	23 M –	25 p4 47 m	– –	– –
<i>Macaca sp.</i>	I, C 43 P3/P4 69 M1/M2/M3 1 maxilla (P3–M2)	i, c 3 p3, 10 p4 16 m1/m2, 15 m3 1 mandible (d2/m1/m2)	– – – –	– – – –
Colobinae indet.	31 M1/M2/M3	5 m2, 1 m3	–	–
<i>Hylobates sp.</i>	2 M1/M2	1 m1/m2	–	–
<i>Pongo pygmaeus</i>	1 C 2 P3, 2 P4, 1P (?) 6 M1/M2	1 I1, 2 I2 5 p3, 4 p4 5 m1/m2, 1 m3	1 di1 – –	1 dc – –
<i>Homo sp.</i>	1 M1, 1 M3	–	–	–

Some others are fragmentary or highly worn and thus have been determined as “cf.” Many undetermined fragments are not listed. Upper teeth are written with capital letters (P, M, D) and lower teeth with small letters (p, m, d).

produced only 10 teeth, which we attributed to *Nemorhaedus sumatrensis* (Bechstein, 1799) and 2 teeth of the very large bovid *Bubalus cf. bubalis* (Linnaeus, 1758) (Table 3).

Concerning *Nemorhaedus*, M1 and M2 have styles, which are more salient than the pillars of cusps (paracone and metacone). In

one molar, probably an M3, the pillar of the metastyle widens towards the base of the crown to a salient ridge. Tougard (1998) also describes this feature on an upper M3 from Thum Wiman Nakin. The mesostyle and the parastyle are well developed. The posterior lobes are much square in their occlusal outline than the



Fig. 7. Location of sites cited in the text. Vietnam: Tham Kuyen (475 ± 125 ka); Tham Om (250–140 ka) not so different from Hang Hum (140–80 ka) (but with *M. m. cf. margae*, *V. cf. zibetha*, *Homo sapiens*, *Elaphodus* sp., *Paguma larvata*, *Nemorhaedus sumatrensis*); Lang Trang (80–60 ka). Laos: Tam Hang (Middle Pleistocene). Thailand: Thum Wiman Nakin (169 ± 15 ka). Cambodia: Phnom Loang (late Middle Pleistocene).

anterior lobes. The lower molars (1 m1/m2 and 4 m3) conform to the *Nemorhaedus* morphology. The parastylid and the entostylid are more marked than the metastylid.

The dimensions of the teeth (Table 4) are comparable to fossil data from Phnom Loang (Tin Thein, 1974) and Thum Wiman Nakin (Tougaard, 1998) and to modern specimens (Tin Thein, 1974). Once again, the data from Yenchinkuo are not exploitable here because the dimensions given for *Nemorhaedus sumatrensis kanjereus* correspond to rows of teeth only (Colbert and Hooijer, 1953).

Only two teeth, worn and fragmentary, one m1 and one p3, are attributable to a large bovid (Table 3). The m1 has the characteristics of the modern water buffalo *Bubalus bubalis*, the second one is highly worn and probably belongs to the same species.

4.2.3.3. Suids. Numerous isolated teeth can be assigned to *Sus scrofa* Linnaeus, 1758 (146 permanent and 10 milk teeth), and five permanent molars to *Sus barbatus* at Duoi U'O'i. Most jugal teeth are highly worn with completely flat occlusal surface (Table 3).

The P4s are molarised. The lower premolars have the typical *Sus* pattern with cusps aligned in the mesiodistal axis. Most of the jugal teeth are bunodont, with smooth enamel, and resemble those of modern *Sus scrofa*. *Sus barbatus* is morphologically close to *S. scrofa* and distinguishing between the species is difficult. The molars have four cusps and numerous accessory tubercles (Fig. 8). On the molars, the anterior cingulum has numerous star-like folds. The Furchenplan system is developed and the cingulum has numerous styles and stylids. The only feature that allows us to distinguish *S. barbatus* from *S. scrofa* is the ridulated enamel in the former (Tougaard, 1998).

No size difference can be noted between *S. scrofa* and *S. barbatus* in the sample from Duoi U'O'i (Table 4), contrary to

the data from Thum Wiman Nakin (Tougaard, 1998). All the teeth of *S. scrofa* fall within the size range of Lang Trang (de Vos and Long, 1993), Thum Wiman Nakin (Tougaard, 1998) and Yenchingkuo (Colbert and Hooijer, 1953), and Punung for m3 (Badoux (1959) cited by de Vos and Long (1993)). The *S. barbatus* recorded at Thum Wiman Nakin (Tougaard, 1998) is represented by comparable small samples. The available sample of *S. barbatus* from the Niah cave (Medway, 1977; de Vos and Long, 1993) is much larger but its attribution, mainly based on size, remains questionable according to de Vos and Long (1993).

4.2.4. Perissodactyla

The Perissodactyla are represented by rhinocerotids and tapirids (Table 3). Their crown dimensions are presented in Table 5, and some teeth are figured in Fig. 9.

4.2.4.1. Rhinocerotids. Fifty-nine isolated rhino teeth (and teeth fragments) have been recovered in the fossiliferous breccia of Duoi U'O'i (Table 5): 19 teeth are attributed to the great Indian Rhino *Rhinoceros unicornis* Linnaeus, 1758, 26 to the lesser one-horned rhino *Rhinoceros sondaicus* Desmarest, 1822, and 4 to the Sumatran rhino *Dicerorhinus sumatrensis* Fischer, 1814. Three and four lower deciduous teeth are respectively identified at the genus level (*Rhinoceros* sp.) and to Rhinocerotina indet. (i.e. *Rhinoceros* sp. or *Dicerorhinus* sp.). Two permanent molar fragments are attributed to Rhinocerotina indet.

Three distinct morphs observed on M3, m2 and m3 are evidence for the presence of three rhinoceros species at Duoi U'O'i. Concerning M3, the ectometaloph DU27 retains a small posterolabial tubercle as a cingulum, and it shows an inflection anterior to the posterior root, as it is observed only in *D. sumatrensis* (Guérin, 1980, p. 62, Fig. 7C). Besides, DU26 and DU28 are considerably larger than any M3 referred to *D. sumatrensis* (notably DU1073), and they have an anterior constriction on the protoloph, which points to *R. unicornis*; this feature is always lacking in *R. sondaicus* (DU30, DU1081, Guérin, 1980, p. 60). On the other hand, the ectometaloph DU31 presents a convex outline with a thick paracone fold, typical of *R. sondaicus*. The m2 DU24 (*D. sumatrensis*) is very small and narrow (Table 5), with a V-shaped posterior valley, in lingual view. Other m2s, larger and wider and with thick enamel, belong to *R. sondaicus* (DU20) or to *R. unicornis* (DU24). *D. sumatrensis* is represented by four permanent molars (M3, m2 and m3—which may belong to the same old individual), while other species (*R. unicornis* and *R. sondaicus*) are documented both by dozens of milk and permanent teeth originating from several juvenile, subadult and adult individuals.

Among the numerous species referred to as *Rhinoceros* throughout the Quaternary of South Asia, such as *R. sivalensis* Falconer and Cautley, 1868 and *R. kendengindicus* Dubois, 1908, many can be considered as junior synonyms of *R. unicornis* (for synonymy, see Laurie et al., 1983). On the other hand, according to most authors, the Pleistocene species *Rhinoceros sinensis* Owen, 1870 must be considered to be a distinct species, although it “has become a ‘wastebasket’, all the Quaternary rhino fossils from South China being put into it” (Tong, 2001, p. 588). Nevertheless, we do consider this latter species to be a junior synonym of *R. unicornis*. In spite of the scarcity of associated milk teeth in the Pleistocene of South Asia (Hooijer, 1946a,b; Colbert and Hooijer, 1953; Bacon et al., 2004) and the wide intraspecific variability observed in coeval samples (e.g., Colbert and Hooijer, 1953, Figs. 39–40, p. 101), most rhino milk molars from Duoi U'O'i could be identified at the species level, thanks to size (Table 5) and morphological features (such as the presence/absence of a posterior cristid on the metaconid of lower milk teeth).

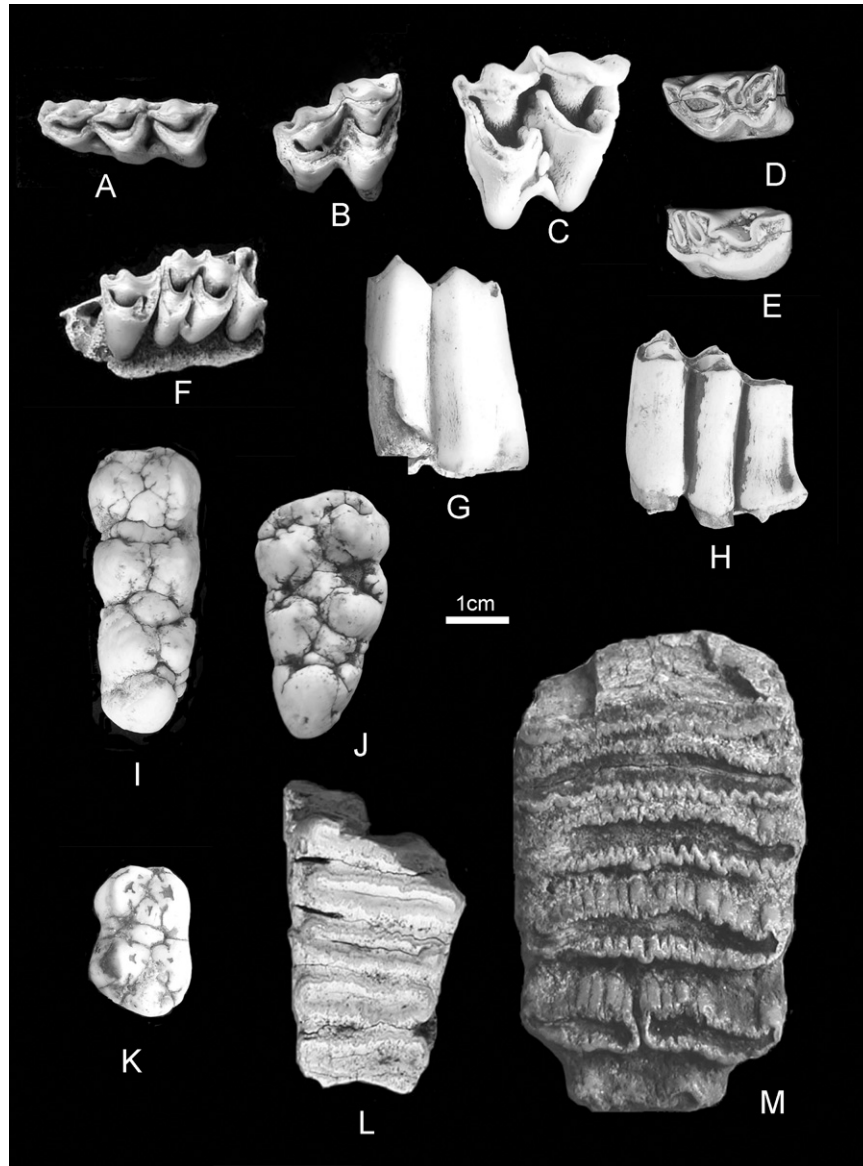


Fig. 8. Artiodactyls and Elephants from Duoi U'Oi. *Cervus unicolor* Kerr, 1792: A. DU393, left d4; B. DU469, left D3; C. DU564, left M1/M2; D. DU921, left p4; E. DU926, right p3. *Muntiacus muntjak* (Zimmermann, 1780): F. DU412, maxilla with left P4/M1. *Nemorhaedus sumatrensis* (Bechstein, 1799): G. DU542, right M3; H. DU569, left m3. *Sus scrofa* Linnaeus, 1758: I. DU766, left m3; J. DU773, left M3; K. DU848, left m2. *Elephas* sp. L. DU639, D2; M. DU632, molar. All are in natural size and in occlusal view, except G (lingual view) and H (labial view).

4.2.4.2. *Tapirids*. The Malay tapir, *Tapirus indicus* Desmarest, 1819, is documented by ten permanent cheek teeth, and a probable D4 (DU42) (Table 5). Although tapirid teeth are easy to distinguish among large ungulate teeth, it is extremely difficult to identify isolated teeth at the species level. Moreover, “P3 and P4, p3 and p4, m1 and m2 are difficult to be distinguished” within a given species (Tong, 2005, p. 148).

According to Colbert and Hooijer (1953, p. 83), the single valid species of the genus *Tapirus* for the Late Pleistocene and Holocene of South Asia is *Tapirus indicus*, for which two subspecies are recognised: the Holocene and extant *T. i. indicus* and the extinct *Tapirus indicus intermedius* Hooijer, 1947. *T. sinensis* (Owen, 1870 and *T. sanyuanensis* Huang, 1991) were also described as present from the Early to Middle Pleistocene and from the Early Pleistocene of China, respectively (Tong, 2005).

All the dental dimensions of the tapir material from Duoi U'Oi (Table 5) correspond to the mean values given by Colbert and Hooijer (1953, Tables 1 and 2: pp. 85–86) for *T. i. intermedius*,

i.e. slightly larger than for *Tapirus indicus indicus*, but much less than those of the extinct giant tapir *Megatapirus augustus* from the Middle Pleistocene of the Indochinese Province (Matthew and Granger, 1923; Hooijer, 1947; Colbert and Hooijer, 1953; Tougaard, 2001).

4.2.5. Proboscidea

The Proboscidea are represented only by ten dental remains (Table 3). Two teeth are illustrated in Fig. 8.

4.2.5.1. *Elephants*. Eight permanent and two deciduous elephant teeth were found at Duoi U'Oi (DU630–639) (Table 6). Most teeth are fragmentary or highly worn and their position in the dentition is difficult to determine. Like all the other mammal remains, the roots of some teeth present post-mortem gnawed facets probably due to porcupines. Among the deciduous teeth are two D2, and among the permanent molars are probably one M1 and two m1, the others being undetermined. However, we can say that in

Table 4

Dimensions of the Duoi U'Oi well-preserved teeth attributed to Artiodactyla: *Cervus unicolor*, *Muntiacus muntjak*, *Nemorhaedus sumatrensis*, *Bubalus cf. bubalis*, *Sus scrofa* and *Sus barbatus* (N: effectives, ranges of length and width)

Teeth	N	Length	Width
<i>Cervus unicolor</i>			
D2	4	17.8–18.9	12.3–12.8
D3	2	19.5–20.3	16.1–18.4
D4	1	19.8	17.8
P2	1	18.5	16.9
P3	1	16.2	18.8
P4	6	14.6–16.4	17–21.8
M1/M2/M3	24	21.1–27.9	19.4–28.6
d4	4	26.7–30.7	11.6–13.1
p2	6	13.9–16	8.8–9.8
p3	4	16.5–20.1	10.1–11.4
p4	13	17.6–20.4	10.1–13.1
m1/m2	15	21.3–26.3	14.5–18.8
m3	18	29.9–38.1	15.9–17.9
<i>Muntiacus muntjak</i>			
D3	2	11.1–11.1	9.5–9.5
D4	11	8.8–11.2	9.7–13
P2	12	8–11	9–12.3
P3/P4	19	7.1–10.8	9.5–13.5
P4	7	7–10	10–13
M1/M2/M3	30	9.2–13.7	10.5–16
d4	2	12.1–13.1	6.1–6.4
p2	2	7.8–8.6	4–5.1
p3/p4	5	9.3–11.1	5.6–7
m1/m2	12	11.4–14.5	7.5–14.7
m3	12	14.1–18.8	7.3–9.6
<i>Nemorhaedus sumatrensis</i>			
M1/M2	4	17.4–19.9	14.5–18.3
M3	1	21.5	14.9
m1/m2	1	16.9	10.7
m3	4	25.4–26.8	10.5–11.6
<i>Bubalus cf. bubalis</i>			
m1	1	30.2	19.2
<i>Sus scrofa</i>			
D4	1	16.3	12
P1	7	7.3–9.8	3.1–4.2
P2	2	10.7–13.2	7.1–7.9
P3	12	13–14.7	8.4–12.1
P4	7	12.6–14.4	11.3–15.7
M1	9	14.6–18	12–15.2
M2	16	19.2–25.1	17.4–21
M3	16	36.3–43.6	19.8–23.2
d2	4	11.6–13	5.1–6
p2	2	11.6–12.3	5.9
p3	14	11.5–14.4	5.5–8.3
p4	12	13.6–16.4	9.8–11.7
m1	7	16.3–19.2	11.6–12.9
m2	14	20.8–24.5	14.8–16.7
m3	18	30.6–46.8	16.4–20.3
<i>Sus barbatus</i>			
M3	2	43.1–43.6	22.1–22.7
m3	2	39.7–40.3	17.3–18.5

general, contrary to the genus *Stegodon* also present in southeast Asia, the enamel is thin with the outer layer much thinner than the inner layer, a feature clearly visible on some teeth, especially deciduous ones, but not measured; between two lamellae, the valleys have a “U” shape; the crown is high as it can be observed on some isolated lamellae of fragmentary molars (DU635–636–637) and the lamellae are aligned across the occlusal surfaces. In one incomplete molar, with only three preserved lamellae (DU634), there is what we suggest to be a posterior median sinus of the enamel loop. Based on this small number of features, we are inclined to assign these teeth to *Elephas* sp. The other parameters that are more useful for species identification such as the number

Table 5

Dimensions of the Duoi U'Oi well-preserved teeth attributed to Perissodactyla: *Rhinoceros*, *Dicerorhinus sumatrensis* and *Tapirus indicus* (N: effectives, ranges of length and width)

Teeth	N	Length	Anterior width	Posterior width
<i>Rhinoceros unicornis</i>				
d1	1	20.5	10.4	10.6
d3	6	40.8–47.4	16.8–19	19.7–22.4
p2	1	31.4	16.7	18.2
p4	4	38.7–50	22.1–26.1	26.3–29.3
m1	2	44.3–46.7	29.9–30.7	30–31.7
m2	1	50	29	28.7
m3	1	59.2	31	30.6
<i>Rhinoceros sondaicus</i>				
D1	1	24.2	20.6	19
D2	1	41.1	34.8	34.4
D3	2	(> 39.8)–44.3	41.2	(34.2)–38.5
D4	1	48.6	–	(> 41)
M1	1	52.5	59.9	–53
M3	1	–	–	52.4
d3	5	39.7–43.2	17–19.1	20.5–22.6
p2	2	(26.5)–28.2	(> 14.6)–15.2	17.2–17.5
p3	2	(34.5)–36.7	21.7–22	23.3–25.2
m1	1	42.5	26.9	28.6
m2	1	43.2	28.6	–
m3	4	49.4–52.6	26.5–28.2	26.8–29.3
<i>Rhinoceros</i> sp.				
d3	1	–	–	21.5
<i>Dicerorhinus sumatrensis</i>				
m2	1	40.4	25.2	25.6
m3	1	45.9	24.8	25.3
<i>Rhinocerotina</i> indet.				
d4	4	–	19.5–22.3	–
<i>Tapirus indicus</i>				
M1/M2	2	27.0–30.8	(31.1)–33.3	28.6–(> 29.2)
p3	1	28.7	(19.8)	(18.2)
m2	2	31.1–32.3	22.3–22.6	20–20.7
m3	2	32.8–34.7	24.3–25.5	20.7–22.3

of lamellae, lamellar frequency, height/width index or hypsodonty index are unknown (Hooijer, 1955; Osborn, 1942; Maglio, 1973; van den Bergh, 1999). Consequently, specific attribution for the species, *Elephas namadicus* or *Elephas maximus* is impossible.

4.2.6. Carnivora

The Carnivora at Duoi U'Oi are diversified (Table 3). They consist of mustelids, canids, viverrids, felids and ursids. Some teeth are figured in Fig. 10.

4.2.6.1. Mustelids. Nine teeth attributed to *Arctonyx collaris* Cuvier, 1825 were recovered at Duoi U'Oi. Among the upper teeth are two I3, two P4, two complete M1, two fragmentary M1, and among the lower teeth only one m1. One P4 is attributed to an undetermined Meline (Table 3).

The two P4 are triangular in their occlusal outline. They display a developed paracone, which is a pointed blade more prominent than the metastyle, a small parastyle and a very small protocone. They conform to the morphology of modern *A. collaris*. The crown of the unidentified P4 (DU91) is larger and its buccal outline is rounded. It exhibits a salient metastyle as high as the paracone. The parastyle is small. The protocone is not visible due to wear of the crown. This tooth is attributed to an unidentified Meline. Indeed, we did not find among modern Asian mustelines a species that could approximate to its pattern. Four upper first molars, two complete crowns and two with only their distal halves, also conform to the morphology of *A. collaris*. They are longer than they

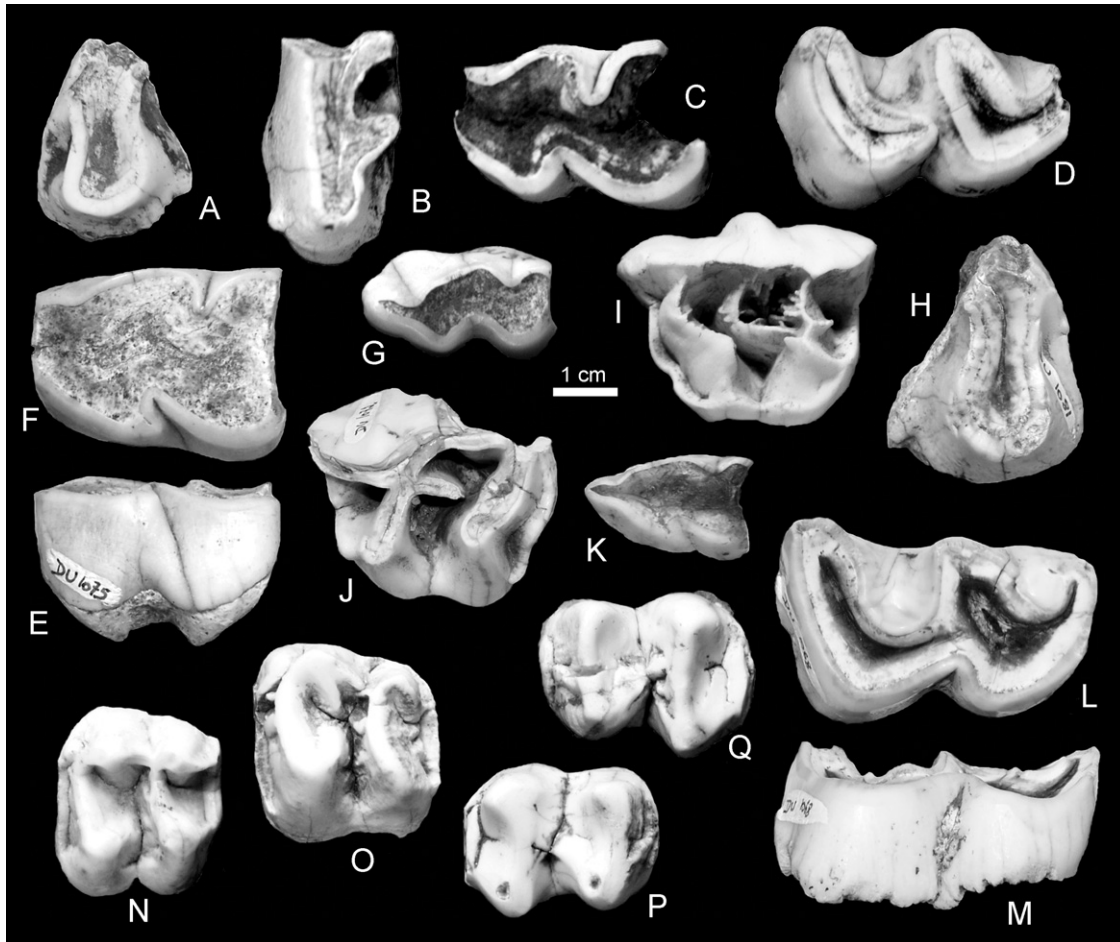


Fig. 9. Perissodactyls from Duoi U'Oi. *Dicerorhinus sumatrensis* (Fischer, 1814): A. DU1073, protoloph of a left M3; B. DU27, ectometaloph of a right M3; C. DU24, left m2; D. DU14, right m3. *Rhinoceros unicornis* Linnaeus, 1758: E, F. DU1075, left p4; G. DU37, left p2. *Rhinoceros sondaicus* Desmarest, 1822: H. DU1081, protoloph of a right M3; I. DU34, left D2; J. DU1072, right D3; K. DU1067, left p2; L, M. DU1068, right m3. *Tapirus indicus* Desmarest, 1819: N. DU47, left M1-2; O. DU48, left M2; P. DU44, right m2; Q. DU51, right m3. All are in natural size and in occlusal view, except F and M (labial view).

are wide. The paracone and the metacone are the most important cusps in size and height on 3 of the teeth whereas the paracone is the higher cusp on the fourth tooth. The two buccal cusps and the posterobuccal cone are not aligned, the latter being shifted towards the inner side of the crown. The three lingual cusps (metaconule, protocone and paraconule) of equal size form a serrated ridge across the occlusal surface. The lingual cingulum is well developed.

P4 and M1 fall within the size range of all modern and fossil specimens from Lang Trang (de Vos and Long, 1993), Thum Wiman Nakin (Tougaard, 1998) as well as Yenchingkuo (Colbert and Hooijer, 1953). Fossils from this latter site are attributed to *Arctonyx collaris rostratus* and are not comparatively larger. It must be noted that the number of all the samples is very small (Table 7).

4.2.6.2. Canids. Twenty-one teeth conform to the dental pattern of the common species *Cuon alpinus* Pallas, 1811 (Table 3). The upper dentition includes nine premolars amongst which are six P4 or carnassials. These are massive teeth with large and developed paracones. The metastyle forms a large blade, which is distally elongated. On most of the crown, the protocone is worn but seems to have been not so developed. Two teeth display a well-marked wear facet running up the ridge of the powerful blade. The M1 is a small-size tooth. The paracone is a large mound, higher than the metacone. The protocone is entirely worn. One complete p4 has the typical three aligned cusps, with a marked cingulum at the

base of the crown. This tooth, as with all the lower dentition, is characteristic of *C. alpinus*.

The dimensions of the Duoi U'Oi teeth (Table 7), except for P4, do not display a marked size difference with that of fossil specimens from Yenchingkuo (Colbert and Hooijer, 1953) attributed to the subspecies *Cuon alpinus antiquus*. This is also the case for the single m1 from Lang Trang (de Vos and Long, 1993). They are quite rather close to modern specimens of *C. alpinus*.

4.2.6.3. Viverrids. Four teeth are attributed to viverrids: one lower premolar is undetermined, one P4 is attributable to *Viverra* cf. *zibetha* Linnaeus, 1758, while the two complete M1 would suggest the occurrence of two species at Duoi U'Oi: *V. zibetha* and *Viverra* cf. *megaspila* Blyth, 1862 (Table 3).

The P4 has a very developed but highly worn protocone, and a very small parastyle. The stout and pointed paracone and the compressed metastyle form two elongated blades. A marked cingulum is present. The first M1 (DU92) close to modern *V. zibetha* has a triangular crown, buccolingually elongated. A parastyle close to the paracone is present. Protocone and metastyle are of the same size. Comparatively, the second M1 (DU1158) is more rectangular in its outline, and much less buccolingually elongated, as observed in modern *V. megaspila* (Table 7). Supplementary material should be necessary for confirming the presence of this taxon, until now never recorded in a Pleistocene site.

Colbert and Hooijer (1953) described a new subspecies at Yenchingkuo *Viverra zibetha expectata*, but the differences with the modern *V. z. ashtoni* concern certain characteristics of the muzzle, palate and auditory bulla rather than the size of the dentition. We note no size differences between the *V. zibetha* teeth from Duoi U'Oi, the *V. z. expectata* teeth from Yenchingkuo and the modern *V. z. ashtoni* teeth.

4.2.6.4. *Felids*. Only a P4 can be attributed to the small felid *Neofelis* cf. *nebulosa* (Griffith, 1821) (Table 3). The protocone is worn. The parastyle is a small mesial cusp situated in the axis formed by the paracone-metastyle blade, as in the modern species. The proportions (length and width) of the tooth suggest a taxonomic attribution to *N. nebulosa* rather than to the other small common felids found in modern Southeast Asian faunas, *Felis temminckii*, *Felis planiceps* and *Prionailurus bengalensis*.

Felids are also represented by two species of *Panthera*, *Panthera pardus* (Linnaeus, 1758) and the large *Panthera tigris* (Linnaeus, 1758). The three p3 and three p4 of *P. pardus* are of simple shape.

Table 6

Principal teeth dimensions of *Elephas* of Duoi U'Oi (according to Maglio, 1973; van den Bergh, 1999)

Tooth	Length	Width	Height	<i>p</i>
M1	> 120	57.5	–	8 ^{1/2}
d2	–	24.8	37.6	4
d2	–	27.9	29.4	4 ^{1/2}
Molar	–	62.9	–	–
Molar	–	41.1	–	–
Molar	–	46.4	–	–
Upper molar	–	56.8	97+	–
m1	–	72.7	100+	–
m1	–	66.7	115+	–

“*P*” is the number of lamellae.

The p4 have three cusps aligned along the mesiodistal axis, the central cusp being the most developed. The cutting edge of the two small m1 consists of two blades (paraconid, protoconid) separated by a notch. Their dimensions are clearly those of *P. pardus* (Table 7). The other m1 is a powerful blade-like carnassial tooth of *P. tigris*. A set of eight canines also conforms to this genus. The size of the teeth falls within the range of fossil specimens, those from Lang Trang for both species (de Vos and Long, 1993), and Yenchingkuo (Matthew and Granger, 1923; Colbert and Hooijer, 1953) and Punung (Badoux, 1959) for *P. tigris*. Modern specimens of *P. tigris*, the only ones available (Colbert and Hooijer, 1953), are slightly smaller.

4.2.6.5. *Ursids*. Twenty-two teeth clearly have the characteristics of *Ursus thibetanus* Cuvier, 1823, whereas three teeth are more characteristic of the Asian bear *Helarctos malayanus* (Table 3).

The three P4 display well-developed paracones and metastyles (metacones according to de Vos and Long, 1993), the latter being wide blades as in *U. thibetanus*. The protocone (deuterocone according to de Vos and Long, 1993) is not visible, the occlusal surface on the lingual side being highly worn. Two M1 are large mesiodistally as in *U. thibetanus*; the paracone and the metacone are equal in size; the parastyle and the metastyle are well marked, and the hypocone and the protocone form a thin mesiodistal blade. The third M1 is smaller and has dimensions close to those of *H. malayanus*. The three M2, longer than they are wide, with a distally elongated talonid, conform to the *U. thibetanus* pattern. One of the teeth presents a crenulated cingulum. The main cusps, paracone and metacone, form a sharp crest, unlike the lingual cusps. The two m1 are triangular in shape and not elongated like *H. malayanus*. The trigonid is pointed whereas the talonid is large (buccolingual width taken between hypoconid and hypoconulid). A deep notch separates the two areas. The protoconid is well developed and more anterior than the metaconid. The m2 is wider posteriorly than anteriorly (as in

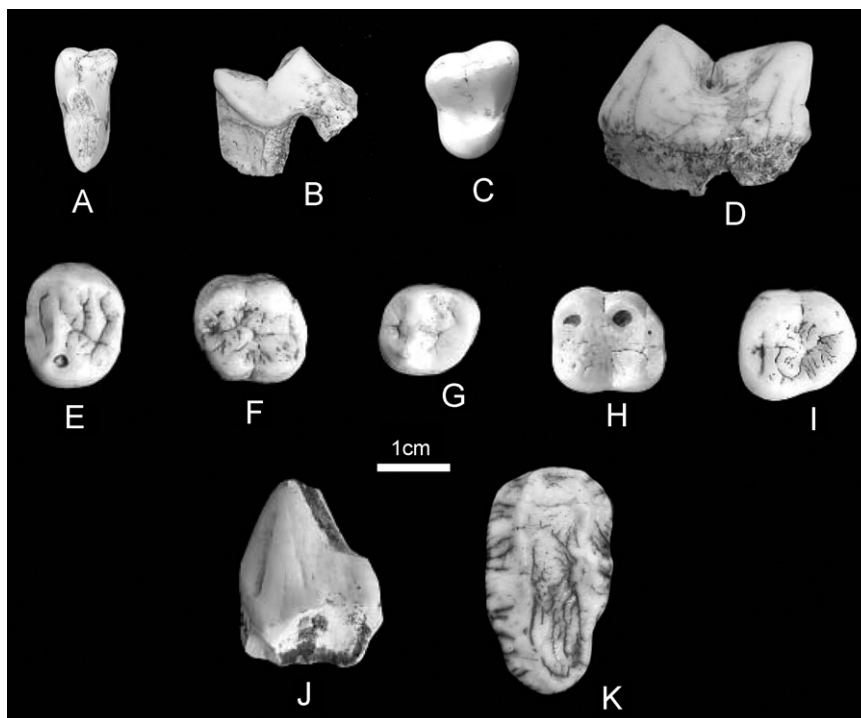


Fig. 10. Carnivores and Primates from Duoi U'Oi. *Cuon alpinus* Pallas, 1811: A. B. DU65, right P4; C. DU70, right M1. *Panthera tigris* (Linnaeus, 1758): D. D707, right m1. *Pongo pygmaeus* (Linnaeus, 1760): E. DU1007, left P4; F. DU1013, left M1; G. DU1010, left p4; H. DU1009, right m1/m2; I. DU996, right m3; J. DU1005, left C. *Ursus thibetanus* Cuvier, 1823: K. DU59, left M2. All are in natural size and in occlusal view, except B and D (lingual views).

Table 7Dimensions of the Duoi U'Oi well-preserved teeth of Carnivora (*N*: effectives, ranges of length and width)

Taxa	Teeth	<i>N</i>	Length	Width
<i>Arctonyx collaris</i>	P4	2	9.3–9.8	7.3–7.6
	M1	3	17–17.3	11.1–11.9
	m1	1	15.7	6.3
Melinae indet.	P4	1	10.7	8.3
<i>Cuon alpinus</i>	P1	1	6.3	4.3
	P2	1	7.1	3.7
	P3	1	13.5	6
	P4	4	19–21.6	8.5–10.7
	M1	1	11.8	14.3
	p1/p2	5	6.3–8	3.2–3.8
	p3/p4	4	12.1–12.8	5.7–7.1
	m2	2	6–6.7	8.5–8.7
	M2	1	7.5	7.3
Carnivora indet.	M2	1	7.5	7.3
<i>Viverra cf. zibetha</i>	P4	1	13	6.7
<i>Viverra zibetha</i>	M1	1	7.1	12.7
<i>Viverra cf. megaspila</i>	M1	1	7.1	10.4
Viverridae indet.	p	1	6.37	4.56
<i>Neofelis cf. nebulosa</i>	P4	1	17.3	–
<i>Panthera pardus</i>	p3	3	11–13.3	5.1–7.3
	p4	2	14.1–15.8	6.7–8.2
	m1	2	13.6–14.7	6.4–6.5
	m1	1	26.3	14.4
<i>Panthera tigris</i>	m1	1	26.3	14.4
<i>Ursus thibetanus</i>	P4	3	11.6–13.1	9.5–11.2
	M1	3	15.1–18.1	10.6–13.6
	M2	3	26.9–31	15.4–17.2
	m2	1	20.5	12
	m1	2	16.9–18.2	9.7–11.3

the description of *Ursus thibetanus kokeni* by Colbert and Hooijer (1953).

For the teeth dimensions (Table 7), the comparison between data from Duoi U'Oi with those of modern (mainly *U. thibetanus*) and fossil specimens, *U. thibetanus* (Lang Trang, Thum Wiman Nakin), *U. t. kokeni* (Yenchingkuo) and *H. malayanus* (Lang Trang), do not show marked differences. In particular it is impossible to justify the validity of *U. t. kokeni* (Matthew and Granger, 1923; Colbert and Hooijer, 1953), in comparison with the new data (de Vos and Long, 1993; Tougard, 1998).

4.2.7. Rodents

4.2.7.1. Hystricids. The Rodents are represented only by large teeth attributed to hystricids (Table 3). Ninety-five porcupine teeth complete the record for the mammals. Among these are 23 worn upper molars and 72 lower teeth (25 p4, 47 molars) (Table 8). Most of the molars are highly worn and could not be measured. Their morphology resembles that of modern *H. brachyura* Linnaeus, 1758. The length and width ranges of the lower premolars and molars are closer to those of Lang Trang (de Vos and Long, 1993) rather than to those of modern specimens (Bacon et al., 2006). Indeed, the fossil specimens (both from Lang Trang and Duoi U'Oi) appear to be larger than the modern ones.

4.2.8. Primates

The Primates at Duoi U'Oi consist of cercopithecids, colobids, hylobatids, pongids and hominids (Table 3).

4.2.8.1. Cercopithecids. Many of the specimens are attributed to an undetermined macaque (Table 3): 115 isolated upper teeth, among which are 3 D2, 44 isolated lower teeth, but also two jaw fragments, a maxilla with P3/P4/M1/M2 and a mandible with d2/m1/m2, the only ones recovered among all the fauna. To these elements may be added a set of incisors and canines, most of them

Table 8Dimensions of the Duoi U'Oi well-preserved teeth of Primates and Rodents (*N*: effectives, ranges of length and width)

Taxa	Teeth	<i>N</i>	Length	Width	
<i>Hystrix brachyura</i>	p4	22	7.2–9.1	5.5–7.3	
	m1/m2	30	8.4–11.9	6.5–9.8	
	m3	4	7.3–9	6.2–6.5	
<i>Macaca</i> sp.	D2	3	6.6–8.6	5.1–8.6	
	P3/P4	43	4.4–11.8	4.1–6.8	
	M1/M2/M3	69	7.6–10.2	7.1–10.2	
	p3	3	8.8–9.6	4.9–5.4	
	p4	10	5.9–7.4	4.5–5.4	
	m1/m2	16	7.3–9.7	5.7–7.4	
	m3	15	10.2–12.4	6.4–7.5	
	Colobinae indet.	M1/M2/M3	31	5.8–7.7	5.2–6.7
		m2	5	6.5–7.5	5.3–5.9
m3		1	9.4	6	
<i>Hylobates</i> sp.	M1/M2	2	6.3–6.7	7.1–7.6	
	m1/m2	1	7.7	5.8	
<i>Pongo</i> sp.	dc	1	–	–	
	di1	1	14.02	9.4	
	P3	2	10.9–11.6	13.6–14	
	P4	2	11–12.8	14.2–16.7	
	M1/M2	6	11.6–15.7	12.2–15.3	
	I1	1	9.6	9.6	
	I2	2	8.3–8.9	7.8–9.5	
	p3	5	14.1–16.4	9.3–11.2	
	p4	4	11.9–13.8	10.8–12.5	
	m1/m2	5	14–15.8	12.2–15.2	
	m3	1	16.7	15.1	
<i>Homo</i> sp.	M1	1	12	12.9	
	M3	1	10.5	12	

worn and fragmentary, characteristic of *Macaca*. In comparison with the carnivores, the upper canines display a mesial marked groove and the lower canines an enlarged distal cingulum.

P3 and P4 are bicuspid. The posterior fossa is larger than the anterior one and the preprotocrista is consequently mesial, a feature found in *Macaca assamensis* for example and not in *Macaca mulatta* (Tougaard, 1998). The upper molars are bilophodont. The crowns are large near the cervix. The cusps are high (however less high and pointed than in Colobines) with, in ascending order, paracone, metacone, hypocone and protocone. The anterior lophe is always larger than the posterior one. We can sometimes observe the presence of an interconulus and on one tooth (probably an M3) the presence of a distoconulus. The p3 conform to the sectorial form of *Macaca*. Some teeth attributed to males present an extension of the mesial flange below the alveolar plane, whereas some others attributed to females do not present this feature. The p3 are all pointed (sharp) with, on the lingual side, two small fossae separated by a protocristid. The p4 are of simple shape with two mesial cusps. The distal fossa, the talonid, sometimes has two cusps (hypoconid and entoconid). The lower molars are rectangular in shape. Some m3 have a tuberculum sextum (between the entoconid and the hypoconulid). The dimensions of teeth (Table 8) show large overlaps with those of macaques from the other sites.

4.2.8.2. Colobids. Thirty-one upper molars and five lower molars are attributed to one unidentified colobine (Table 3). In comparison with *Macaca*, the teeth of Colobinae are smaller, with high and sharp cusps. The molars are bilophodont. The systematics for Asian colobines (langurs) vary according to the authors (Corbet and Hill, 1992), we prefer to cautiously retain an attribution to Colobinae indet. Size dimensions are given in Table 8.

4.2.8.3. Hylobatids. Only three teeth (two upper molars and one lower molar, m1 or m2) can be attributed to the genus *Hylobates*. The upper molars are small teeth and there are no features that

permit them to be attributed to one species. The only lower molar has the Y-5 pattern, and its cusps are highly worn (Table 3). The dimensions of teeth (Table 8) show large overlaps with those of hylobatids from the other sites.

4.2.8.4. Pongids. Thirty-two teeth, 2 deciduous and 30 permanent, are attributed to *Pongo pygmaeus* (Linnaeus, 1760) (Table 3). For three teeth (DU753–758–760), the status of *Homo* remains questioned. For most of them, the roots have been gnawed by porcupines (Fig. 10).

Among the 10 permanent upper teeth, the canine conforms to the shape and size pattern for modern *P. pygmaeus* males. The mesial side is rounded, whereas the distal side displays a large wear facet. The lingual face is slightly concave and has a vertical groove from the tip to the base. Close to this groove, the enamel forms a vertical pillar up to the tip of the crown. Two P3 have worn occlusal surfaces, so the marginal ridges are not visible. One tooth seems to have a preprotocrista from the paracone to the protocone. Two P4 are clearly distinguished by size, the small one having more numerous and distinct crenulations and wrinkles. The paracone and the metacone are slightly shifted mesially, so that the distal part of the crown is larger. The mesiodistal axis of the teeth is covered by a deep developmental groove (Swindler, 1976). Six upper molars, three intact and three worn, are M1 or M2 with four main cusps. They do not have vestigial cusps (metacone and hypocone) as in M3. On one tooth, the metacone is the highest cusp, suggesting an M1 (Swindler, 1976), whereas on two other teeth the metacone is as high as the paracone, suggesting an M2. Postprotocrista and deep mesiodistal developmental grooves are present and visible even in the worn teeth. Additional transverse cristae delimit the mesial and distal fossae. A sulcus obliquus is present. It is a groove that separates the hypocone from the other cusps and descends to the lingual surface of the crown. Among the 18 permanent lower teeth, three incisors (one i1 and two i2) have the characteristics of *P. pygmaeus*. The apex of the central incisor is worn. The lingual cingulum is bent. The two lateral incisors are asymmetrical, with small crenulations on the lingual surface. The five p3 display an important size difference. All are sectorial with a large and mesiodistally elongated protoconid, very bent on its buccal face. The metaconid is small and is connected to the protoconid by a transverse crest, the protocristid (Swindler, 1976). On the lingual surface, we can observe two fossae: the mesial trigonid and distal talonid basins. The four p4 have the same size and morphology. The metaconid faces a smaller protoconid and joins it by a protocristid. The talonid basin varies in shape within the set of p4: it can be rounded and wide or quite small with an entoconid. This variability has already been observed in modern and fossil specimens (Hooijer, 1948; Bacon and Long, 2001; Swindler, 1976). Six lower molars, among which one is fragmentary, are listed. Five are probably m1 or m2 and one an m3. According to Swindler (1976), the position of the tooth on the dental row may be determined: “On M₁ the metaconid is either slightly distal to or opposite the protoconid, whereas on M_{2–3} the metaconid more frequently faces the protoconid”.

The teeth from Duoi U’Oi would include 3 m1/m2 and one m1. We find all the characteristics of *P. pygmaeus*: a high metaconid; the presence of a protocristid; and a variable position of the hypoconulid (distobuccal or distolingual). The m3 is triangular in shape. It has a small talonid in comparison with the trigonid. The talonid presents three cusps.

As there is a wide overlap in teeth size between modern *P. p. pygmaeus* and *P. p. abelii* (Ushida, 1996) and the fossil subspecies, some of which are questionable (Hooijer, 1948; Badoux, 1959; Groesbeek in de Vos and Long, 1993; Schwartz et al., 1994, 1995), we retain for the Duoi U’Oi teeth a general attribution to *P. pygmaeus*.

4.2.8.5. Hominids. We identified two *Homo*-like teeth, one left M1 (DU761) and one right M3 (DU757) (Table 8). The occlusal surface of the M1 is highly worn but with a discernable trace of the paracone, the hypocone and the middle part of the oblique ridge. The crown is broader buccolingually (12.9 mm), than it is mesiodistally (12 mm). The tooth has three partly gnawed roots, two buccal fused and a single lingual one. The M3 shows only the paracone. The other cusps and the oblique ridge are highly worn. The three roots (two buccal and one lingual) are gnawed. The teeth are too worn and fragmentary to be attributed to species level (*sapiens* or *erectus*), using the standard method.

5. Discussion

5.1. The composition of the Duoi U’Oi fauna: some comments on the systematics

The Duoi U’Oi fauna (Table 3) consists of modern taxa with most animals still living in the same area, or elsewhere in Southeast Asia (Corbet and Hill, 1992).

Most of the teeth could be assigned to one species, as they have already been described for Pleistocene sites and are not very different from their modern counterparts. The taxonomic attribution of some of the other teeth is however limited to the genus level due to the difficulty in recognising species (de Vos and Long, 1993; Bacon et al., 2004). This concerns *Macaca*, *Hylobates*, *Homo* and *Elephas*. The *Macaca*, the species living in the Indochinese area (*M. nemestrina*, *M. assamensis*, *M. arctoides*, *M. mulatta*, *M. fascicularis* according to Corbet and Hill, 1992), present dental similarities in their morphology, and size overlaps. The problem is the same for the *Hylobates* (*H. lar*, *H. pileatus*, *H. gabriellae*, *H. hollock*, *H. leucogenys*, *H. syndactylus* (Corbet and Hill, 1992)). Isolated primate teeth are attributed here to undetermined species, although we must point out that previously some authors have attempted taxonomic assignments (e.g., Kahlke, 1961; de Vos, 1983, 1985; Cuong, 1985; Olsen and Ciochon, 1990; Chaimanee and Jaeger, 1993; Harrison, 1996; Tougaard, 1998; Storm et al., 2005).

This task is also difficult because of controversy over the taxonomic ranking of modern species. The problem of living Asian colobines often raised in the literature is particularly significant, as their generic identity is still unresolved. In general, the classifications define four genera *Trachypithecus*, *Semnopithecus*, *Pygathrix* and *Presbytis*, but the species differ according to the authors (Corbet and Hill, 1992; Lekagul and McNeely, 1988; Oates et al., 1994). The issue of the attribution of highly worn human teeth (*Homo* sp.), which has been previously assessed at Ma U’Oi (Demeter et al., 2004, 2005), is recurrent with the Duoi U’Oi elements. Finally, the two species of *Elephas* that might have been present in this area during the Pleistocene (*E. maximus* and *E. namadicus*) are mainly defined on the basis of cranial characteristics (Hooijer, 1955; Maglio, 1973; van den Bergh, 1999), and as the isolated teeth of Duoi U’Oi are fragmentary, the species is undetermined (*Elephas* sp.).

In terms of systematics, the archaic subspecies have been mainly defined in the first 50 years of the 20th century, principally because first discoveries mainly concerned Middle Pleistocene assemblages. Indeed, most of the first elements recovered (teeth or skull) when compared with modern forms were found to be slightly bigger (Matthew and Granger, 1923; Hooijer, 1947; Colbert and Hooijer, 1953), even if later discoveries showed large overlaps between extinct and extant forms. The badger *A. c. rostratus* was defined at Yenchingkuo, a Middle Pleistocene site, because of its differences in size and form compared to the modern species *A. collaris collaris* (Matthew and Granger, 1923; Colbert and

Hooijer, 1953). In the same way, one may cite *U. t. kokeni* (Matthew and Granger, 1923) larger than the modern *U. thibetanus*; *T. i. intermedius* Hooijer, 1947 “since the dimensions of the (Sumatran) cave teeth are intermediate between those of the recent Sumatran tapir and those of the Pleistocene *Tapirus augustus* Matthew and Granger from Wanshien, province of Szechwan, China”; *Muntiacus muntiacus margae* Hooijer, 1951, larger than modern Chinese forms (Colbert and Hooijer, 1953); *N. s. kanjereus* Colbert and Hooijer, 1953 “like modern *Capricornis sumatraensis* but larger” (Colbert and Hooijer, 1953, p. 127); and *R. sondaicus guthi* Beden and Guérin, 1973, a subspecies named for its larger size in comparison with modern and fossil *R. sondaicus* known at this time. Among the small carnivores, *C. a. antiquus* (Colbert and Hooijer, 1953) was created on the basis of large and robust dentition compared with that of *C. alpinus alpinus*, the northern dhole. Finally, concerning *V. z. expectata* Colbert and Hooijer, 1953, differences with the modern counterparts *Viverra zibetha ashtoni* concern the skull and brain case rather than the size of dentition.

This trend towards a multiplication of archaic subspecies has been carried farther with *Pongo*. Hooijer (1948) had first initiated this process when he described two extinct subspecies, *P. pygmaeus weidenreichi* from southern China and *P. p. palaeosumatrensis* from Sumatra on the basis of size and dental proportions. For Hooijer (1948, p. 187), *P. p. palaeosumatrensis* was defined from isolated teeth (recovered in different Early Holocene Sumatran sites), which are larger than those of extant *P. pygmaeus* (composed of *P. p. pygmaeus* from Borneo and *P. p. abelii* from Sumatra). The teeth attributed to *P. p. weidenreichi*, defined from isolated teeth recovered at Hoshangtung, are larger than those of extant and extinct orangutans (Hooijer, 1948, p. 280). Later, Schwartz et al. (1994, 1995) described four new subspecies in Vietnam, each allocated to one site, on the basis of the same criteria defined by Hooijer (1948): *P. p. ciochoni* (Lang Trang), *P. p. devosi* (Hang Hum), *P. p. fromageti* (Tham Om) and *P. p. kalkei* (Tham Kuyen). They also defined a new species, *P. hooijeri* (Schwartz et al., 1995).

Since the first determinations of Pleistocene faunas, subspecies have not been fully accepted even though slight metrical differences exist between living and fossil specimens (Badoux, 1959; Kahlke, 1972; Groesbeek in De Vos and Long, 1993; Bacon and Long, 2001, 2002). However, the differences are sufficient to justify the infraspecific level.

5.2. Biostratigraphical interest of the Duoi U'O'i fauna

As the radiometric framework is still poorly documented, the Duoi U'O'i contribution is important. Around the transition between the Middle and the Late Pleistocene, well-dated faunas are rare (Table 9). Concerning the continental sites, Thum Wiman Nakin in Thailand (Ginsburg et al., 1982; Chaimanee and Jaeger, 1993; Tougard, 1998, 2001; Esposito et al., 1998; Esposito, 2002), and recently Ma U'O'i (Bacon et al., 2006) are the only sites where radiometric datings have been processed. The other sites are dated on the basis of faunal compositions: Lang Trang in Vietnam (Long et al., 1996), and Phnom Loang in Cambodia (Carbonel and Guth, 1968; Beden et al., 1972; Beden and Guérin, 1973; Tin Thein, 1974).

The Duoi U'O'i faunal composition has all the characteristics of a Late Pleistocene mammalian assemblage and its biochronological age is consistent with U/Th dating (66 ± 3 ka). In this respect, it resembles faunas of relatively the same age, Lang Trang (80–60 ka) (de Vos and Long, 1993; Long et al., 1996) and the slightly older Hang Hum (140–80 ka) (Cuong, 1985; Olsen and Ciochon, 1990). However, Duoi U'O'i is devoid of archaic components found to be present on those sites, such as *Stegodon orientalis* at Lang Trang (Table 10), or *E. namadicus*, *S. orientalis*, *M.*

augustus and *S. lyddekeri* at Hang Hum. It is also devoid of archaic subspecies, particularly present at Hang Hum (Cuong, 1985), *T. i. intermedius*, *M. m. margae*, *U. t. kokeni*, *C. a. antiquus*, *A. c. rostratus*, *N. n. primigenia*.

It is obvious that archaic subspecies are common in the middle Middle Pleistocene, and that their numbers begin to decrease in the late Middle Pleistocene and then decrease dramatically in the Late Pleistocene. To illustrate these three periods, among the 29 taxa recorded at Yen-chingkuo (Colbert and Hooijer, 1953), 14 are assigned to archaic subspecies. For Thum Wiman Nakin, we count 5 subspecies for 27 taxa (Tougaard, 1998), whereas among the 22 taxa recorded at Lang Trang, only one is a subspecies (de Vos and Long, 1993; Long et al., 1996). The record of Duoi U'O'i suggests that, ca 66 ka, modern subspecies are settled in this area. Duoi U'O'i is thus the oldest well-dated modern fauna known for the Indochinese province. Its originality lies in its totally modern aspect.

The Duoi U'O'i fauna also illustrates the paleostratigraphy of some species (Tables 9 and 10). This is the case for the bearded pig *S. Barbatus*, which was, until now, only described on the mainland in the late Middle Pleistocene of Thailand at Thum Wiman Nakin around 169 ka (Tougaard, 1998, 2001; Esposito et al., 1998; Esposito, 2002). Its occurrence at Duoi U'O'i confirms that this species was still present in the Indochinese region at 66 ka. Duoi U'O'i also records the first undeniable *R. unicornis* since only *R. cf. unicornis* had been reported so far in the late Middle Pleistocene in North Vietnam and Thailand (Tougaard, 2001; Bacon et al., 2004). It is then the first co-occurrence of the three recent Asian rhinocerotid species on a Late Pleistocene Indochinese site, and the radiometric age is consistent with the modern affinities of these perissodactyls.

5.3. Affinity of the Duoi U'O'i fauna with those of the sundaland

The resemblance of the Duoi U'O'i fauna to those of coeval localities such as Punung (two localities) (Von Koenigswald, 1939, 1940; Badoux, 1959; de Vos, 1983) and Gunung Dawung in Java (Storm et al., 2005; Storm and de Vos, 2006), Lida Ajer, Sibrambang and Djambu caves in Sumatra (Hooijer, 1947; de Vos, 1983) is striking (Fig. 11, Table 9). All these sites are considered to be of relative same age, even though some dates are still debated. According to authors, Punung is estimated to be 80–60 ka (Skelton and de Vos, 1985), or recently 126–81 ka (Storm, 2001). Most elements present at Duoi U'O'i also occur in these Sondaic sites. Indeed, they are composed of modern faunas with migrants like *P. pygmaeus*, *H. syndactylus*, *H. malayanus*, *E. maximus*, *N. sumatrensis*, *S. scrofa* and *S. barbatus* (de Vos, 1983). The strongest faunal similarity is, however, between Duoi U'O'i and Sibrambang in Sumatra, the closest island from the Malay Peninsula (Fig. 11). In comparison with the fauna at Sibrambang, that of the other Sumatran site Lida Ajer does not include *B. bubalis*, *P. tigris* and *R. sondaicus* (de Vos, 1983), and those of Punung and Gunung Dawung in Java appear as impoverished versions (Badoux, 1959; de Vos, 1983, 1985, 1995; van den Bergh et al., 2001; Storm et al., 2005; Storm and de Vos, 2006). Among the 21 taxa present at Sibrambang, only 15 are recorded at Punung and 10 at Gunung Dawung (Table 9).

It seems that, at the time of Duoi U'O'i, ca 70 ka, the Sundaland was mainly characterised by faunas of modern aspect. The presence of *Pongo* at Duoi U'O'i, as well as at Punung and Sibrambang, implies that at this time, tropical forests may have expanded across a wide area of the Sundaland. Even if the vegetal cover of the Sundaland was supposed by some authors not to be so homogeneous during times of connection (see Heaney, 1991; Meijaard, 2003; Bird et al., 2005 for a review about this question),

Table 9
Comparison of the Duoi U'O'i faunal list with those of the most documented Late Pleistocene sites

	Thailand Thum Wiman Nakin 169 ± 15 ka	Vietnam Lang Trang Late Pleistocene	Vietnam Duoi U'O'i 66 ± 3 ka	Java Ngandong Late Pleistocene	Java Punung I and II 80–60 ka	Java Gunung Dawung 80–60 ka	Sumatra Lida Ajer 80–60 ka
<i>Cervus unicolor</i>	X	X	X	–	–	–	X
	–	–	–	<i>Cervus</i> sp.	–	? <i>Cervus</i> sp.	–
<i>Muntiacus muntjak</i>	X	X	X	X	X	X	X
<i>Nemorhaedus sumatrensis</i>	<i>N. s. cf. kanjererus</i>	X	X	–	X	–	X
<i>Bubalus bubalis</i>	X	X	X	–	–	–	–
	–	–	–	<i>B. palaeokerabau</i>	<i>Bubalus</i> sp.	–	–
<i>Sus scrofa</i>	X	X	X	–	<i>S. vittatus</i>	<i>Sus</i> sp.	X
<i>Sus barbatus</i>	cf.	–	X	–	X	–	X
	–	–	–	<i>S. macrognatus</i>	–	–	–
	–	–	–	? <i>S. brachygnatus</i>	–	–	–
<i>Rhinoceros unicornis</i>	Cf.	–	X	–	–	–	–
<i>Rhinoceros sondaicus</i>	X	X	X	–	X	X	–
<i>Dicerorhinus sumatrensis</i>	–	X	X	–	–	–	X
<i>Tapirus indicus</i>	<i>T. i. cf. intermedius</i>	X	X	X	X	X	X
<i>Elephas</i> sp.	–	X	X	–	–	–	–
	<i>E. cf. maximus</i>	–	–	<i>E. hysudrindicus</i>	<i>E. maximus</i>	–	<i>E. maximus</i>
<i>Arctonyx collaris</i>	<i>A. c. rostratus</i>	X	X	–	–	–	X
<i>Cuon alpinus</i>	–	X	X	–	–	–	X
<i>Viverra zibetha</i>	–	–	X	–	–	–	–
<i>Viverra megaspila</i>	–	–	X	–	–	–	–
<i>Neofelis nebulosa</i>	–	–	X	–	–	–	–
<i>Panthera pardus</i>	–	X	X	–	–	–	X
<i>Panthera tigris</i>	–	X	X	–	–	–	–
<i>Ursus thibetanus</i>	X	X	X	<i>P. tigris</i> ssp.	<i>P. t. sondaica</i>	–	–
<i>Helarctos malayanus</i>	–	X	X	–	X	X	X
<i>Hystrix brachyura</i>	?	X	X	?	X	X	X
<i>Macaca</i> sp.	<i>M. cf. nemestrina</i>	<i>M. mulatta</i>	X	<i>M. fascicularis</i>	<i>M. nemestrina</i>	–	X
	–	<i>M. arctoides</i>	–	–	–	–	–
Colobinae indet.	–	–	X	–	–	–	X
	<i>Trachypithecus</i> sp.	<i>Presbytis</i> s. l.	–	–	–	<i>Trachypithecus</i> sp.	–
<i>Hylobates</i> sp.	–	X	X	–	<i>H. syndactylus</i>	<i>H. syndactylus</i>	X
<i>Pongo pygmaeus</i>	–	X	X	–	X	X	X
<i>Homo</i> sp.	X	–	X	<i>H. erectus</i>	? <i>H. sapiens</i>	–	? <i>H. sapiens</i>

Thum Wiman Nakin in Thailand (Tougaard, 1998; Esposito et al., 1998); Lang Trang in Vietnam (de Vos and Long, 1993; Long et al., 1996), Ngandong (de Vos et al. (1984) on the basis of data from Von Koenigswald (1933, 1934) and Aziz (1989), the two localities of Punung (Badoux, 1959; de Vos, 1983, 1985; van den Bergh et al., 2001), and Gunung Dawung (Storm et al., 2005) in Java, and Lida Ajer in Sumatra (de Vos, 1983, 1995). The fauna of Sibrambang in Sumatra is the same as that of Lida Ajer but it can be added *Bubalus bubalis*, *Panthera tigris* and *Rhinoceros sondaicus* (de Vos, 1983).

Table 10
Comparison of faunal lists of the Late Pleistocene sites including the other taxa not present at Duoi U'Oi:

	Thailand Thum Wiman Nakin 169 ± 15 ka	Vietnam Lang Trang Late Pleistocene	Vietnam Duoi U'Oi 66 ± 3 ka	Java Ngandong Late Pleistocene	Java Punung I and II 80–60 ka	Java Gunung Dawung 80–60 ka	Sumatra Lida Ajer 80–60 ka
<i>Axis porcinus</i>	X	–	–	–	–	–	–
Cervidae indet.	X	–	–	X	X	–	–
<i>Cervus eldii</i>	X	–	–	–	–	–	–
<i>Bibos</i> sp.	–	–	–	–	X	–	–
<i>Bibos paleosondaicus</i>	–	–	–	X	–	–	–
<i>Bos sauveli</i>	X	–	–	–	–	–	–
<i>Bos javanicus</i>	X	–	–	–	–	–	–
<i>Bos frontalis</i>	X	–	–	–	–	–	–
Bovidae indet.	–	–	–	–	–	X	–
<i>Hexaprotodon sivalensis</i>	–	–	–	X	–	–	–
<i>Stegodon orientalis</i>	–	X	–	–	–	–	–
<i>S. trigonocephalus</i>	–	–	–	X	–	–	–
<i>Crocuta crocuta ultima</i>	X	–	–	–	–	–	–
<i>Ailuropoda melanoleuca</i> <i>baconi</i>	X	X	–	–	–	–	–
<i>Martes flavigula</i>	X	–	–	–	–	–	–
<i>Paguma larvata</i>	X	–	–	–	–	–	–
<i>Paradoxurus</i> <i>hermaphroditus</i>	X	X	–	–	–	–	X
<i>Felis temmincki</i>	–	X	–	–	–	–	X
<i>Lutra perspicillata</i>	–	X	–	–	–	–	–
<i>Echinosorex</i> sp.	–	–	–	–	X	–	–

Thum Wiman Nakin in Thailand (Tougaard, 1998; Esposito et al., 1998); Lang Trang in Vietnam (de Vos and Long, 1993; Long et al., 1996), Ngandong (de Vos et al. (1984) on the basis of data from Von Koenigswald (1933, 1934) and Aziz (1989), the two localities of Punung (Badoux, 1959; de Vos, 1983, 1985; van den Bergh et al., 2001), and Gunung Dawung (Storm et al., 2005) in Java, and Lida Ajer in Sumatra (de Vos, 1983, 1995).

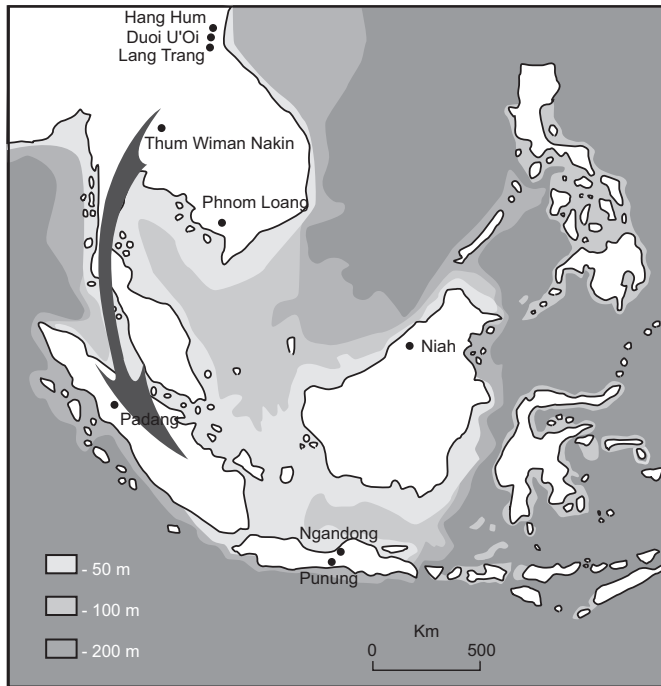


Fig. 11. Map of the Sundaland showing different sea levels (–50 m, –100 m, –200 m) from van den Bergh et al. (1996). We have figured some late Middle Pleistocene sites (Hang Hum, Thum Wiman Nakin) and Late Pleistocene sites (Duoi U'O'i, Lang Trang, localities from Padang Highlands (Lida Ajer, Sibrambang and Djambu), Punung and Niah cave). The arrow indicates the dispersal route for mammals at a sea level of –50 m.

the migration of forest-dependent species, such as *Pongo* or *Hylobates*, requires the continuous presence of forest to survive. We follow the hypothesis of van den Bergh et al. (1996, 2001) who stipulate that the immigration of this modern fauna might take place during the later part of Oxygen Isotopic Stage 5 (OIS5), roughly between 110 and 70 ka, when sea level was about 50 m below its present level and sufficient to connect large islands (Borneo, Java, Sumatra) to the Malay Peninsula (Voris, 2000), and warm and humid climatic conditions still prevailed (prior to 70 ka but after the glacial maximum at 135 ka) (Chappell and Shackleton, 1987; Prentice and Denton, 1988) (Fig. 11).

The biostratigraphy of Java shows an important faunal turnover, the modern fauna contrasting with previous ones (Trinil, Kedung Brubus, Ngandong), which rather represented an open woodland environment (de Vos et al., 1982; de Vos, 1983; Sondaar, 1984; Leinders et al., 1985; van den Bergh et al., 2001; Bouteaux, 2005).

5.4. The Duoi U'O'i fauna and its paleogeographical significance

In Figs. 12–14, we have represented modern and past distributions of some of the species present at Duoi U'O'i. The three rhinocerotids, still extant in Asia (Nowak, 1999; Tougard, 2001), evolved during the Pleistocene and the Holocene in different ways as it is shown in Fig. 12. During the late Middle Pleistocene, *R. sondaicus*, *R. unicornis* and *D. sumatrensis* occurred throughout the mainland (Beden et al. 1972; de Vos and Long, 1993; Long et al., 1996; Bacon et al., 2004, 2006). The three species present differences in their distributions during the Pleistocene. *R. sondaicus* and *D. sumatrensis* do not exhibit dramatic changes between the past and the present, whereas *R. unicornis* moved towards the north of India where it remained confined. The presence of *R. unicornis* at Duoi U'O'i confirms, in the past, a more southern geographical range.

On the other hand, *Tapirus indicus* moved to the south (Fig. 12), into a territory which now extends from Burma to Sumatra (Corbet and Hill, 1992). Two other species, *S. barbatus* and *P. Pygmaeus*, moved southwards (Fig. 13). The current distribution of *Sus* is limited to Malaya, Sumatra, Borneo and throughout most of the Philippines, whereas that of *Pongo* is much more restricted, on Sumatra and Borneo (Corbet and Hill, 1992).

Among the carnivores (Fig. 14), *U. thibetanus*, frequent on the mainland during the Pleistocene, never reached the Indonesian islands, but extended far into the north along the Himalayas, up to Afghanistan and Pakistan and into northeastern China (Matthew and Granger, 1923; Young, 1932; Colbert and Hooijer, 1953; Cuong, 1985; de Vos and Long, 1993; Tougard, 1998). *H. malayanus* is present in all Asia since the Late Pleistocene and probably disappeared in Java at the beginning of the Holocene as it is absent in the faunal list of Wajak (van den Brink, 1982; de Vos, 1995). *Panthera pardus* and *Panthera tigris* are widespread, from Bangladesh to Yunnan, in India, in parts of Burma, Thailand, Vietnam, Laos, Cambodia and Indonesia (Sumatra and Java) (Corbet and Hill, 1992). Their distributions show no dramatic changes between the past and the present. Contrary to herbivores, they are less affected by environmental changes.

5.5. Taphonomy

The sequence of events that led from living animals to fossil assemblages in the karstic network is complex. The sedimentological analysis of the Duoi U'O'i cave shows that the fossiliferous deposits represent several thousand years of accumulation. This accumulation resulted from selective factors that are different in nature.

First, almost all the finds, whatever their size from macaque to elephant and even humans, are isolated teeth with characteristic wear facets and gnawed roots indicating porcupine activity. After Nowak (1999), “bones are frequently found in and around burrows they dig themselves, in caves and rock crevices, probably having been carried there, and gnawed to obtain calcium and to hone the incisor teeth”. Porcupines use to recover bones of carcasses after carnivores have finished. In any case, no mark on the teeth can be attributed to human action. This taphonomic characteristic is common in the Indochinese and Sondaic areas and has been observed on Pleistocene sites mentioned here, Lang Trang (de Vos and Long, 1993; Long et al., 1996), Thum Wiman Nakin (Tougaard, 1998), Punung, Sibrambang, Lida Ajer, Gunung Dawung (Badoux, 1959; de Vos, 1983; Storm et al., 2005; Storm and de Vos, 2006), Ma U'O'i (Bacon et al., 2004, 2006), Ban Fa Suai cave (Zeitoun et al., 2005). The porcupine (*Hystrix brachyura*) is still common on all the southeastern sites and its current distribution is widespread (Corbet and Hill, 1992).

Secondly, the absence of small-sized mammals, such as insectivores, bats, small carnivores or rodents, as well as amphibians and small reptiles, suggests a selective preservation of fossils. Indeed, water was the major taphonomic agent responsible for the transport and deposition of the teeth within fissures and galleries, and this transport by strong water flows destroyed and flushed away small elements and preserved only the resistant ones. That would explain why only adult and juvenile teeth of large and middle-sized mammals have been preserved at Duoi U'O'i. The preservation of the fossil material of microvertebrates (teeth but also skeletal elements in general) necessitates a deposition under different sedimentological conditions. This fossilisation bias has been already observed at Ma U'O'i cave, a nearby site, which yielded two clearly different faunas, one mainly composed of middle-sized and large mammals, and one composed of microvertebrates only (Bacon et al., 2006). As we sieved

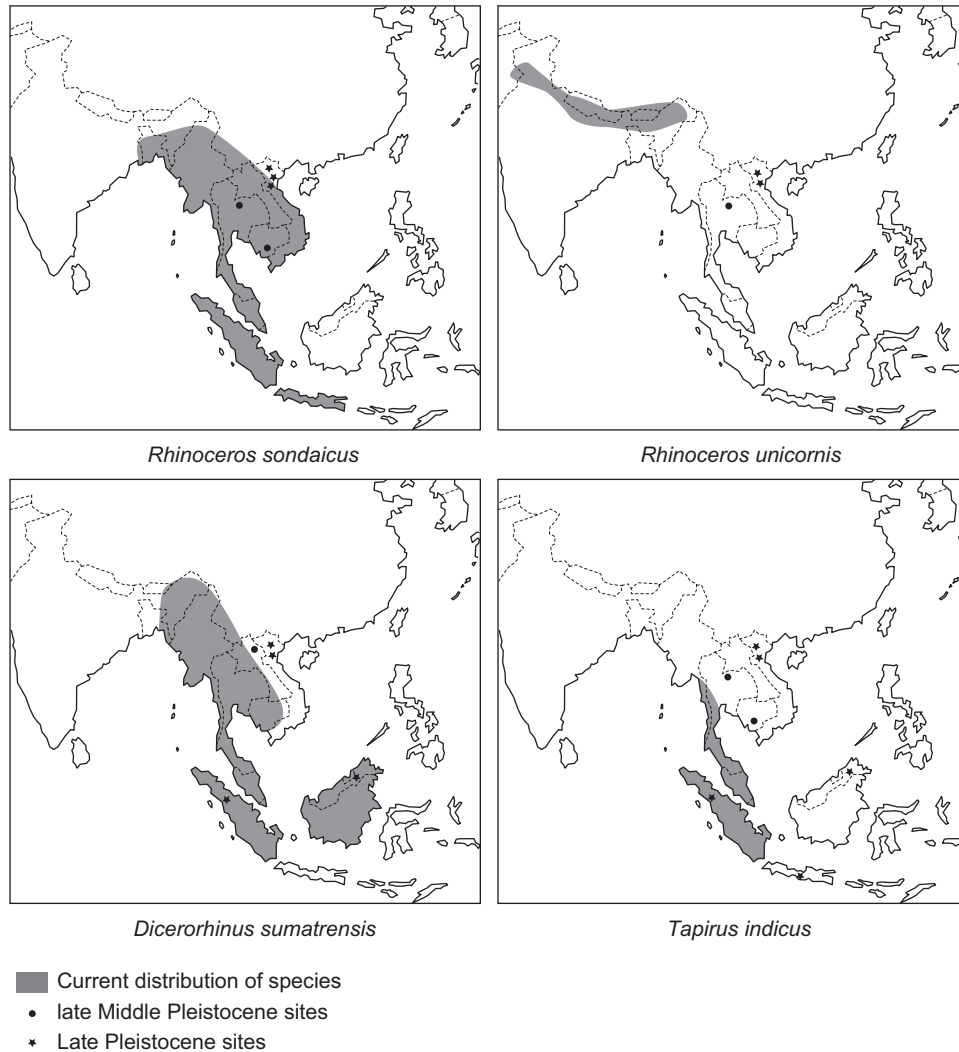


Fig. 12. Current and past distribution of perissodactyls (*R. sondaicus*, *R. unicornis*, *D. sumatrensis*, *T. indicus*). Distributions of modern species are from Corbet and Hill (1992). Distributions of fossil species concern the late Middle Pleistocene sites, Thum Wiman Nakin (Tougaard, 1998), Phnom Loang (Beden et al., 1972; Beden and Guérin, 1973) and Tam Hang (Beden et al., 1972), and Late Pleistocene sites, Duoi U'Oi (this paper), Ma U'Oi (Bacon et al., 2004, 2006), Lang Trang (de Vos and Long, 1993; Long et al., 1996), Punung, Lida Ajer, Sibrambang (de Vos, 1983; van den Bergh et al., 2001), Gunung Dawung (Storm et al., 2005) and Niah cave (Harrison, 1996). *Rhinoceros sondaicus*: Phnom Loang (*R. sondaicus guthi*), Thum Wiman Nakin, Ma U'Oi (*R. cf. sondaicus*), Lang Trang; *Dicerorhinus sumatrensis*: Tam Hang south, Lang Trang, Lida Ajer, Sibrambang, Niah; *Rhinoceros unicornis*: Thum Wiman Nakin (*R. cf. unicornis*), Ma U'Oi (*R. cf. unicornis*); *Tapirus indicus*: Thum Wiman Nakin (*T. indicus cf. intermedius*), Lang Trang, Punung, Lida Ajer, Sibrambang, Gunung Dawung, Niah).

all the fossiliferous sediment at Duoi U'Oi, the absence of microvertebrates is clearly a product of taphonomy.

The demographic composition of the samples observed, based on the biological age of individuals (adult and juvenile), indicates the selective role of predators (here dhole, tiger and leopard), prior to that of porcupines mentioned above. The minimum number of individuals of large mammals is 14 for *M. muntjak* (8 adults and 6 juveniles), 17 for *C. unicolor* (14 adults and 3 juveniles), 16 for *S. scrofa* (12 adults and 4 juveniles), and 4 for *P. pygmaeus* (3 adults and 1 juvenile) (Table 11). In comparison to the biological composition of these species, that of the rhinocerotids with a high proportion of the juveniles is particularly unexpected, and has been studied in detail by one of us (P-O Antoine). The minimum number of individuals is 12 (11 left d3 are attributed to juvenile individuals of *Rhinoceros* sp. and at least one adult of *D. sumatrensis* is recorded). In order to characterise individual ages, the wear stages of 51 teeth have been identified (the last 6 teeth of the sample were not usable for that purpose), following a procedure adapted from Hillman-Smith et al. (1986) for extant white rhinos, as to our knowledge no tooth wear

statistics exist for Asian rhinos. The rhino sample as a whole illustrates a series of individuals ranging from newborn calves aged ca 2–4 months (d3 DU5, *R. unicornis*; d3 DU9, *R. sondaicus*) up to old individuals aged ca 40 years (m3 DU1068, *R. sondaicus*; m2 DU24, *D. sumatrensis*). The rhino series can be split into three groups: (1) a juvenile series, including 18.50 specimens out of 51 (36.3%), with a perfect Gaussian distribution and a peak of 12–18-month-old calves (ca 8 specimens); (2) a subadult series, including 6.18 specimens (12.1%), with a low peak at 4–7 years (4 specimens); (3) an adult series, with 26.32 specimens (51.6%) and a high peak of 20–28-year-old adults (ca 7 specimens) (Fig. 15).

If we focus on the 47 specimens attributed to *Rhinoceros*, the percentages are 39.3% (juveniles), 13.4% (subadults) and 47.4% (adults). This structure differs from what is observed in recent natural populations of Indian rhinos from Nepal (27% juveniles, 21% subadults and 52% adults; Laurie, 1982; Laurie et al., 1983): the calves largely outnumber their theoretical number ($\chi^2 = 8.76$; $p < 0.01$). The Duoi U'Oi *Rhinoceros* "population" structure, artificially young, is biased by an external biotic factor (predation,

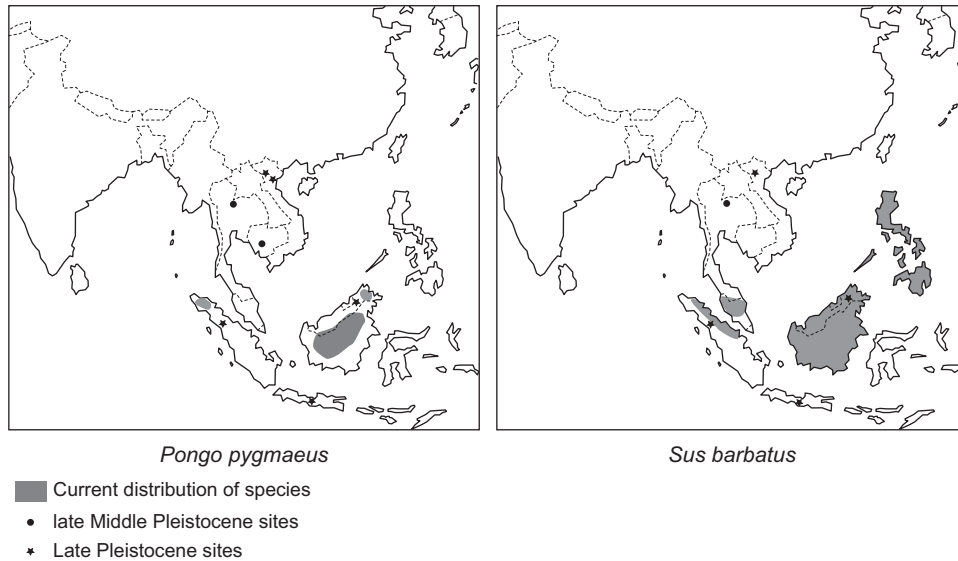


Fig. 13. Current and past distribution of *Pongo pygmaeus*, and *Sus barbatus*. Distributions of modern species are from Corbet and Hill (1992). Distributions of fossil species concern the late Middle Pleistocene sites, Thum Wiman Nakin (Tougaard, 1998) and Phnom Loang (Beden et al., 1972; Beden and Guérin, 1973), and Late Pleistocene sites, Duoi U'Oi (this paper), Ma U'Oi (Bacon et al., 2004, 2006), Lang Trang (de Vos and Long, 1993; Long et al., 1996), Punung, Lida Ajer, Sibrambang (de Vos, 1983; van den Bergh et al., 2001), Gunung Dawung (Storm et al., 2005) and Niah cave (Harrison, 1996). *Sus barbatus*: Thum Wiman Nakin (*S. cf. barbatus*), Punung, Lida Ajer, Sibrambang, Niah; *Pongo pygmaeus*: Thum Wiman Nakin, Phnom Loang, Lang Trang, Punung, Lida Ajer, Sibrambang, Gunung Dawung, Niah.

scavenging), rather than an abiotic factor (hydrodynamics, granulometry): the teeth are not eroded, but some appear to have been gnawed.

On the other hand, the whole rhino sample consists of 59 teeth, with only 18 upper teeth for 41 lower teeth, which indicates also the occurrence of an external biasing factor ($\chi^2 = 8.97$; $p < 0.01$), such as the post-mortem action of porcupines, as it is frequently observed in the Pleistocene cave deposits of South Asia. Predation is not very likely as a prominent accumulation factor, since even tigers rarely assault calves aged more than 6 months (Laurie et al., 1983).

5.6. Species diversity and paleoenvironmental implications

The analysis of ecological diversity in the Duoi U'Oi mammal assemblage is limited, as the material available for study is far from being complete. The major taphonomic factors, such as the selective role of predators and porcupines, selective destruction of age classes for some species, and selective preservation of fossils due to deposition processes in the karstic network contribute to the poor representation of the diversity of the fauna, especially in number of species for certain groups (Table 12). In particular the assemblage does not contain a whole category of small mammals (with a body size less than 500 g), such as insectivores, rodents, small carnivores etc. In comparison with the Thum Wiman Nakin assemblage, the only Southeast Asian late Middle Pleistocene fauna characterised by a richness of species, especially of small and medium-sized mammals (Chaimanee and Jaeger, 1993; Chaimanee, 1998; Tougaard, 1998), that of Duoi U'Oi appears to be very under-representative. An analysis of ecological diversity, by means of histograms (Fleming, 1973; Andrews et al., 1979) or cenograms (Valverde, 1964, 1967; Legendre, 1986, 1989), will be thus poorly informative, as already mentioned by Tougaard and Montuire (2006) for Pleistocene Asian sites.

An advanced palaeoenvironmental analysis cannot be carried out on the Duoi U'Oi mammal assemblage, but some general ecological trends can be observed. In Table 12, we have compiled

the percentages of identified isolated teeth and species for each Order. For species proportions, the higher percentages are those of Carnivora (34.6%), Artiodactyla (23%) and Primates (19%). The numbers of species of Artiodactyla and Primates suggest a forested environment. The presence of numerous Carnivora also suggests an open environment that supposes that the habitat may have been mixed. Their proportion is particularly important in the Duoi U'Oi fauna. Indeed, they only represent 8.7% of material (76 elements among the 866 identified), but constitute 34.6% of all of the faunal diversity (9 species among a total of 26).

Secondly, the presence of *Pongo*, *Hylobates* and also *H. malayanus* clearly indicates humid forest conditions (de Vos, 1983, 1984; de Vos et al., 1994; van den Bergh et al., 1996, 2001; Storm and de Vos, 2006). According to Nowak (1999, p. 615), “the orang-utan appears to be well adapted to several different types of primary forests, ranging from swamps and others areas near sea level to mountainous forests at around 1,500 meters.” “Gibbons occur throughout the deciduous monsoon and evergreen rain-forest of the islands and mainland of Southeast Asia (Nowak, 1999, p. 611)”. Both are mostly frugivorous, but their diet also includes other kinds of vegetation (but also eggs, insects and small vertebrates) according to the availability of fruit resources.

Jablonski and colleagues (2000) showed that, in China, during the Pleistocene, distributions of fossil Pongidae and Hylobatidae changed more strongly with the decrease in areas of tropical and subtropical zones than other catarrhines. Hominoids differ markedly from cercopithecoids in their life history parameters (age of first birth, duration of gestation and weaning periods, duration of interbirth interval, food preference, etc.). However, as cited by these authors (id, p. 153): “While hylobatids managed to maintain distributions in marginal subtropical environments throughout the Pleistocene, pongids did not”. Indeed, the combination of a large body size and a large brain size that requires a high-energy food most of the time (such as ripe fruits regularly found in tropical forests) is a disadvantage when surviving in habitats with extreme seasonality (see van Schaik et al., 1993; Jablonski et al., 2000; Hartcourt and Schwartz, 2001; for a detailed bibliography about this subject). In contrast, the

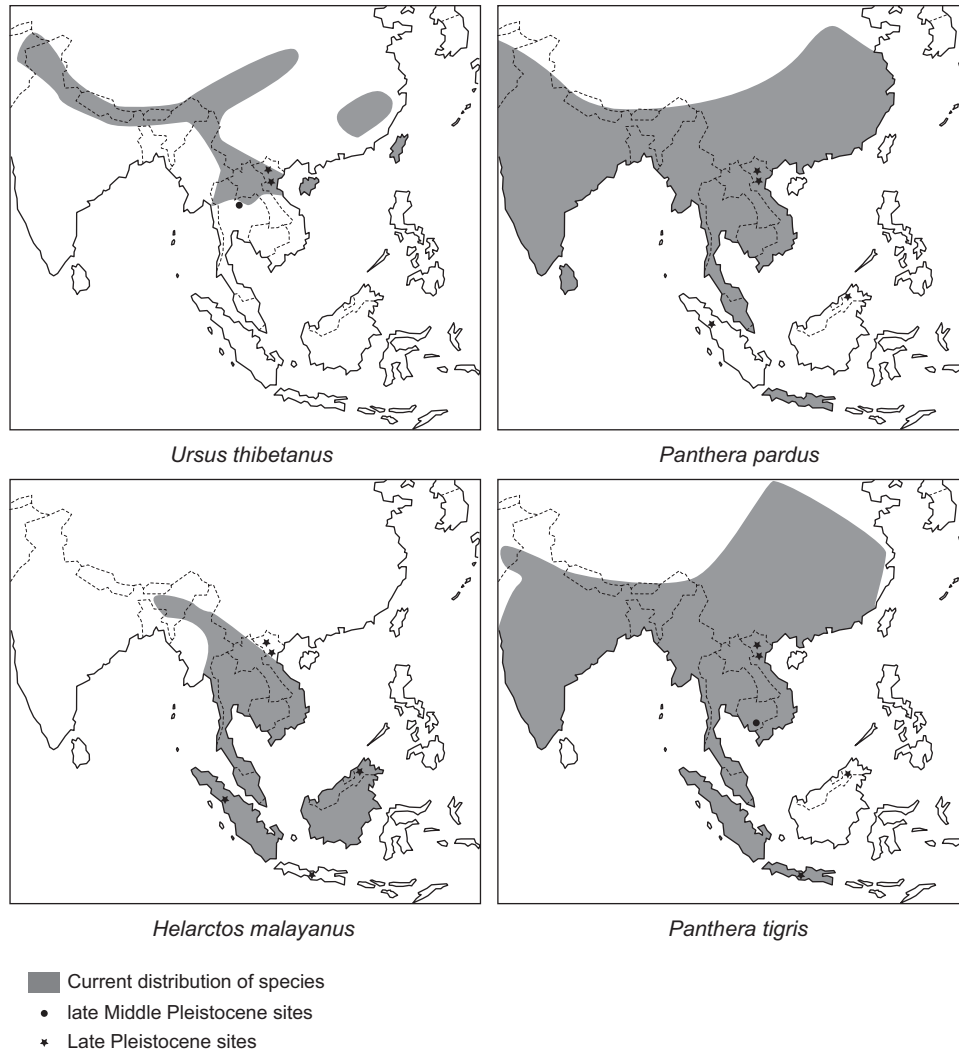


Fig. 14. Current and past distribution of *Ursus thibetanus*, *Helarctos malayanus*, *Panthera pardus* and *Panthera tigris*. Distributions of modern species are from Corbet and Hill (1992). Distributions of fossil species concern the late Middle Pleistocene sites, Thum Wiman Nakin (Tougaard, 1998) and Phnom Loang (Beden et al., 1972; Beden and Guérin, 1973) and Late Pleistocene sites, Duoi U'O'i (this paper), Ma U'O'i (Bacon et al., 2004, 2006), Lang Trang (de Vos and Long, 1993; Long et al., 1996), Punung, Lida Ajer, Sibrambang (de Vos, 1983; van den Bergh et al., 2001), Gunung Dawung (Storm et al., 2005) and Niah cave (Harrison, 1996). *Helarctos malayanus*: Lang Trang, Punung, Lida Ajer, Sibrambang, Gunung Dawung, Niah; *Ursus thibetanus*: Thum Wiman Nakin, Lang Trang; *Panthera tigris*: Phnom Loang, Lang Trang, Punung (*P. tigris sondaica*), Niah; *Panthera pardus*: Lang Trang, Lida Ajer, Niah.

cercopithecoids, which are eclectic feeders, present a greater flexibility in response to environmental stresses (Bennett and Davies, 1994).

The description of a complete skeleton of an adult orang-utan, probably a female, in Vietnam, suggests that subfossil specimens had heavy body weight (Bacon and Long, 2003). This would be an additional argument for a high sensitivity to environmental changes for these fossil apes. From a behavioural point of view, on the basis of field study (Sugardjito and van Hoof, 1986) of modern populations, large body weights do not necessarily signify that fossil forms were more terrestrial (as proposed by Smith and Pilbeam, 1980). Heavy animals more often practice swinging through trees than quadrupedal walking, and travel and rest in low strata of the canopy (between 10 and 20 m), but rarely higher.

Based on these informations, the presence of *Pongo* at Duoi U'O'i suggests that at 66 ka, the north of Vietnam was still covered by subtropical to tropical zones. The other species recovered at Duoi U'O'i suggest, in comparison with their modern counterparts, various kinds of habitats, but these also always include forests and

wooded areas. For example, *Tapirus indicus* lives in tropical moist forests and swamp areas from the Malayan Peninsula and Sumatra, which are rarely found above 1500 m in altitude. It inhabits various types of forest, ranging from dry dipterocarp to deciduous or evergreen forests, according to the season. It is a typical browser feeding on grasses, aquatic plants, leaves, buds, twigs and fruits (Brooks et al., 1997; Nowak, 1999). The omnivorous *H. malayanus* inhabits dense forests at all elevations (Lekagul and McNeely, 1988), and *U. thibetanus* frequents moist deciduous forests and bushy areas, especially in the hills and mountains (Nowak, 1999). *C. unicolor* and *M. muntjak* prefer wooded areas (Nowak, 1999).

As it has been already observed for Southeast Asian fossil faunas from the Middle (Tham Kuyen, Yenchingkuo) and Late Pleistocene (Punung, Lida Ajer, Lang Trang, Niah) (Tougaard and Montuire, 2006), the Duoi U'O'i assemblage is characterised by the abundance of megamammals (at least three species of rhinocerotids, an undertermined species of *Elephas*, *Bubalus bubalis*, *Tapirus indicus*), which suggests humid conditions. According to these

Table 11
Number and percentage of elements of the Duoi U'O'i fauna for each taxon

	MNE	%	MNI	Age
<i>Cervus unicolor</i>	99	11.4	17	14 adults, 3 juveniles
<i>Muntiacus muntjak</i>	114	13.1	14	8 adults, 6 juveniles
<i>Nemorhaedus sumatrensis</i>	10	1.1	2	2 adults
<i>Bubalus bubalis</i>	2	0.2	1	1 adult
<i>Sus scrofa</i>	156	18	16	12 adults, 4 juveniles
<i>Sus barbatus</i>	5	0.5	2	2 adults
<i>Elephas sp.</i>	10	1.1	3	2 adults, 1 juvenile
<i>Rhinoceros unicornis</i>	19	2.1	7	3 adults, 4 juveniles
<i>Rhinoceros sondaicus</i>	26	3	10	5 adults, 5 juveniles
<i>Rhinoceros sp.</i>	3	0.3	3	1 adult, 2 juveniles
<i>Dicerorhinus sumatrensis</i>	4	0.4	1	1 adult
Rhinocerotina indet.	6	0.6	2	2 juveniles
<i>Tapirus indicus</i>	11	1.2	3	2 adults, 1 juvenile
Herbivores	462	53.5	81	–
<i>Arctonyx collaris</i>	9	1	3	3 adults
<i>Cuon alpinus</i>	21	2.4	4	4 adults
<i>Viverra zibetha</i>	1	0.1	1	1 adult
<i>Viverra cf. megaspila</i>	1	0.1	1	1 adult
<i>Neofelis cf. nebulosa</i>	1	0.1	1	1 adult
<i>Panthera pardus</i>	8	0.9	2	2 adults
<i>Panthera tigris</i>	1	0.1	1	1 adult
<i>Ursus thibetanus</i>	22	0.9	3	3 adults
<i>Helarctos malayanus</i>	2	0.2	2	2 adults
Carnivore indet.	9	1	–	–
Carnivores	76	5.9	18	–
<i>Macaca sp.</i>	156+2	18.2	11	9 adults, 2 juveniles
Colobid	37	4.2	8	8 adults
<i>Hylobates sp.</i>	3	0.3	2	1 adult
<i>Pongo pygmaeus</i>	32	3.6	4	3 adults, 1 juvenile
Primates	230	26.5	25	–
<i>Hystrix brachyura</i>	95	10.9	–	–
Total	866	–	–	–

All elements consist of isolated teeth except the two fragmentary jaws of *Macaca*. MNE is the Minimum Number of Elements (identifiable isolated teeth); MNI is the Minimum Number of Individuals. Bold signifies the sums of data.

authors, these humid conditions existed in this area from the Middle Pleistocene in Vietnam (Tham Kuyen is dated to 475 ± 125 ka, Ciochon et al., 1996), and also far to the north, in South China (Yenchingkuo might have the same age as Tham Kuyen, according to the faunal similarities).

Unlike these faunas, whose large mammals are mainly bovids (*Bubalis bubalis* and several species of *Bos*), that of Duoi U'O'i is characterised by a great diversity in rhinocerotids. However, we cannot conclude whether this absence of bovids results from a taphonomic bias, or whether the ecological niches available to large mammals are only occupied by rhinocerotids in particular in this locality. They indicate a wide variety of habitats. Indeed, extant *R. unicornis* inhabits riverine grasslands and marshy areas bordered by woodlands, drier sal forest, or tropical almond forest. In the past, the Indian rhino was recorded in a number of habitats, including marshy lowland, with tall grass or bushes, and occasionally streams and swamps, thick tree and scrub riverine forest and dry, mixed forest (Laurie et al., 1983; Nowak, 1999). The Indian rhino is a grazer, mainly feeding on grass (70–89% of the diet, which also includes fruits, leaves, branches of trees, and shrubs). The Indian rhino drinks daily and visits salt licks regularly (Laurie et al., 1983; Nowak, 1999). *R. sondaicus* prefers tall grass and lowland reed beds in tropical rain forests with a good supply of water and plentiful mud wallows (for bathing). The Javan rhino is an exclusive browser, feeding on shoots, twigs, young foliage and fruits (Nowak, 1999). Lastly, *D. sumatrensis* is found in a wide variety of habitats, from lowland rain forests and swamps to mountain moss forests, but always near water and salt licks. The

Sumatran rhino is a browser (feeding on leaves, twigs and fruits). Seasonal dispersals are recorded, in relation with monsoon regimes (Groves and Kurt, 1972; Nowak, 1999).

The Duoi U'O'i faunal assemblage suggests at 66 ka a forested area and some open habitats, under warm and humid conditions. The pollen collected at Duoi U'O'i is too scarce to provide further information on palaeoenvironments and palaeoethnobotany, the poor preservation of the spores and the pollen in the deposits being the principal cause.

This mosaic of habitats dominated by humid forests is consistent with paleoclimates suggested by palynological records. In this respect, we can quote the conclusion of Tougard and Montuire (2006) about faunas from Sundaland as it can also be applied to that of Duoi U'O'i (Tougaard and Montuire, 2006, p. 135): "Palynological records covering OIS5 indicate warm and humid conditions (rainfall ca 2000 mm) with the expansion of tropical lowland rainforest, humid mid and upper montane forests, fern and woodland cover in eastern Java (van der Kaars and Dam, 1995; van der Kaars et al., 2000) and the dominance of fagaceous monsoon evergreen forest in southern China (Zheng and Lei, 1999)".

5.7. The identification of hominids

The two Duoi U'O'i highly worn teeth assigned to the genus *Homo* do not reveal the identity of the hominids (*sapiens/erectus*) present at that time (66 ± 3 ka) in that subtropical area, in association with that modern fauna.

At the moment, no evidence indicates that *H. erectus* was still present on the continent around 66 ka, and its possible presence in Java up to the end of the Late Pleistocene (Swisher, 1997; Swisher et al., 1996), if it is confirmed, might be an endemic evolution.

The presence of *H. sapiens* at Duoi U'O'i is more plausible, even if its arrival in the Indochinese province is also little documented. Two Vietnamese sites dated to the Late Pleistocene, Hang Hum (140–80 ka) and Keo Leng (30–20 ka but according to some authors this age could be older), might yield teeth of *H. sapiens* (Kha, 1976; Long and Du, 1981; Cuong, 1985; Olsen and Ciochon, 1990; Tougaard, 1998). However, their identification with highly worn isolated teeth is not convincing. Early evidence of *Homo sapiens* in mainland Southeast Asia would be lithic assemblages at Kota Tampan site in Malaysia dated to ca 74 ka (Majid, 2003; Barker et al., 2007). In the Sunda shelf, Niah cave (Barker et al., 2007; Hunt et al., 2007), Tabon cave (Dizon et al., 2002; Détroit et al., 2004) and later Wajak (Storm, 2001) confirm the presence of *H. sapiens* since ca 50 ka (approximate age BP at Niah after Gilbertson et al., 2005). Some researchers suggested that this settlement could occur earlier at Punung and Lida Ajer (Hooijer, 1948; de Vos, 1983; Storm et al., 2005). Punung yielded a human tooth re-assigned to *H. sapiens* (Storm et al., 2005), but this assignment is not approved and thus cannot support for the moment the hypothesis that *H. sapiens* reached the Sundaland before this date. The two human teeth from Lida Ajer are not more convincing (Hooijer, 1948; de Vos, 1983).

5.8. The role of hominids in the taphonomic process

No arguments show that humans might have a possible role in the taphonomic process. First, Duoi U'O'i is not a site attesting a human occupation, since no associated artifacts have been recovered in the deposits. Furthermore, there are no bones fragments with cut marks that would suggest human activity, the material being mainly constituted of isolated teeth. In some Middle Pleistocene sites, where karsts have trapped complete

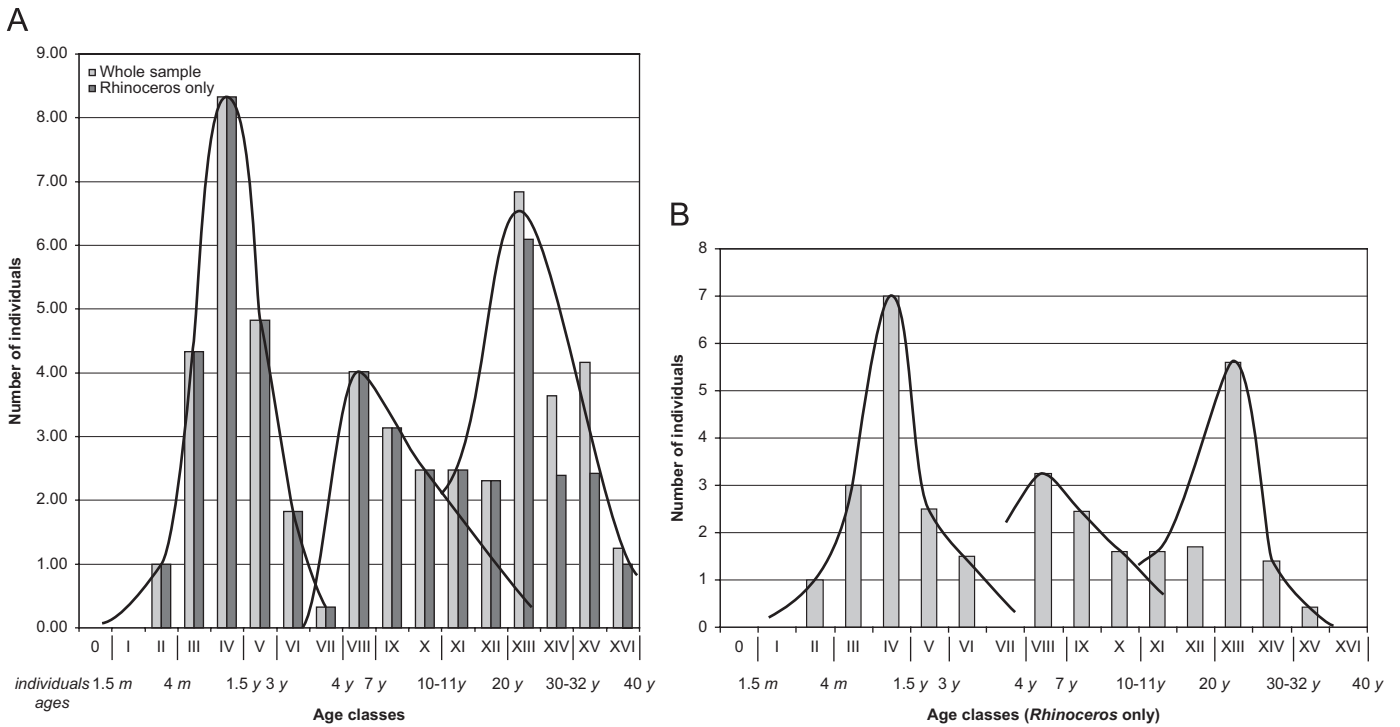


Fig. 15. Age classes hypothesised for the Duoi U’Oi rhinocerotids, based on dental remains, and following a protocol modified from Hillman-Smith et al. (1986). Comparison between the whole rhinocerotid sample (53 teeth: *Rhinoceros unicornis*, *R. sondaicus*, *Rhinoceros* sp., and *Dicerorhinus sumatrensis*; light grey columns), and a sample restricted to *Rhinoceros* (49 teeth: *Rhinoceros unicornis*, *R. sondaicus*, and *Rhinoceros* sp.; dark grey columns). Age classes (O to XVI) and corresponding individual ages in months (m) and years (y), as given by Hillman-Smith et al. (1986).

Table 12
Number and percentage of elements of the Duoi U’Oi fauna for each Order

Groups	MNE	%	NS	%
Artiodactyla	386	44.5	6	23
Perissodactyla	69	7.9	4	15.3
Proboscidea	10	1.1	1	3.8
Total of Herbivores	462	53.5	11	42.1
Carnivora	76	8.7	9	34.6
Rodentia	95	10.9	1	3.8
Primate	230	26.5	5	19
Total of all taxa	866	–	26	–

MNE is the Minimum Number of Elements (only identifiable isolated teeth among the 1189 discovered dental elements); NS is the number of species. The bold signifies the total sum concerning herbivores, carnivores and all taxa.

elements of skeletons, such as Phnom Loang in Cambodia (Beden et al., 1972; Beden and Guérin, 1973) or Yenchingkuo in south China (Matthew and Granger, 1923; Colbert and Hooijer, 1953), the absence of cut marks on bones has also been noted. Secondly, the hominids are components of the assemblage of the fauna, and the wear facet on the teeth due to the porcupine activity shows that they were subject to the same conditions as any mammals. Thirdly, the human remains found associated with animal remains indicate that they were submitted to the same process of deposits in the karstic system.

The question of a possible role of humans in the accumulation of material has already been raised concerning some Pleistocene sites. At Niah cave, the composition of the faunal assemblage, with the presence of burnt bones and cut marks in some fragments of bones, indicates “hunting and processing strategies” (Barker et al., 2007, p. 254). Indeed, considering all elements of the fauna

(number of identifiable specimens among each family), some animals are strongly represented, especially pigs and primates (principally leaf-eating monkeys and macaques, but also orangutans). This record would indicate a selective role of humans. Comparatively, the composition of the mainland Duoi U’Oi fauna reveals marked differences, not only in the proportions of animals but also in its diversity. In order to illustrate those differences, we report in Table 13 the proportions of elements in two continental (Lang Trang, Duoi U’Oi) and two insular sites (Punung, Niah cave). In the latter, in comparison with their overall faunas, the proportions of some groups appear effectively stronger. They concern suids in both sites, but also cercopithecids at Niah and pongines at Punung that would imply hunting technologies adapted to the capture of arboreal primates (Barker et al., 2007). The proportions of the other groups are comparatively insignificant. At Lang Trang and Duoi U’Oi, the proportions of the different groups are much more balanced. The diversity of carnivores and that of some large herbivores is much marked. The only bias observed in the Duoi U’Oi fauna, which concerns age class of the rhinos, could be attributed to the activity of large predators, as well as that of humans, but nothing is sure.

6. Conclusion

The lack of a biostratigraphical framework for the Sundaland is evident. The data being too sporadic, the question of the dispersal into the Sunda shelf of first *H. sapiens* in association with a modern fauna still remains. The Duoi U’Oi fauna, devoid of archaic elements, indicates that this totally modern fauna is present in the Indochinese area since 70 ka, but the identity of the hominid remains to be discovered.

Table 13

Proportions of elements in the faunas from Duoi U'Oï, Lang Trang (Long et al., 1996), Punung (Long et al., 1996) and Niah cave (Barker et al., 2007)

Groups	% Duoi U'Oï	% Lang Trang	% Punung	% Niah cave
Artiodactyla				
Cervidae	24.5	27.4	4.2	0.9
Bovidae	1.3	1.7	0.5	0.2
Suidae	18.5	31.6	>24.6	28.6
Tragulidae	–	–	–	0.8
Perissodactyla				
Rhinocerotidae	6.4	5.8	2.6	–
Tapiridae	1.2	0.5	1.5	–
Proboscidea				
Elephantidae	1.1	0.4	0.2	–
Stegodontidae	–	0.3	–	–
Total of herbivores	53.5	67.7	33.6	30.5
Carnivora				
Felidae	1.1	0.4	1	0.4
Canidae	2.4	0.03	–	–
Viverridae	0.2	–	–	1.2
Mustelidae	1	1	–	0.08
Ursidae	1.1	9.5	0.7	0.08
Total of Carnivores	5.8	10.9	1.7	1.7
Rodentia				
Hystricidae	10.9	11	>24.6	1.5
Primate				
Cercopithecidae	22.6	11	1.1	16.1
Hylobatidae	0.3	0.2	2.9	–
Ponginae	3.6	6.1	14.1	5.9
Total of primates	26.5	17.3	18.1	22

Acknowledgements

We thank the director of the Hoà Binh Museum, Dr. Quach Van Ach, Hoang Thi Thi, Bui Van Khanh, Nguyen Van Dung, and workers from the Tan Lac village. The authors present their gratitude to Mrs. Tran Thi Lan Anh from the NCSH (National Center for Social Sciences and Humanities in Vietnam). Thanks also to Bui Thi Hoi who realized maps of the cave, Annie Bouzheghaia (Université Louis Pasteur) and Danièle Fouchier (UPR 2147) for drawings and graphics. This mission in 2003 was financed by the Direction des Relations Internationales (CNRS), the Laboratoire Dynamique de l'Evolution humaine in Paris (CNRS, UPR 2147), the Collège de France (Pr. Y. Coppens, Chaire de Paléoanthropologie et de Préhistoire), and the Tohoku University School of Medicine, Sendai in Japan (Pr. Y. Dodo).

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