Dated co-occurrence of *Homo erectus* and *Gigantopithecus* from Tham Khuyen Cave, Vietnam

(paleoanthropology/ESR dating/uranium-thorium dating/Pleistocene geochronology)

Russell Ciochon^{*}, Vu The Long[†], Roy Larick[‡], Luis González[§], Rainer Grün[¶], John de Vos[∥], Charles Yonge^{**}, Lois Taylor[¶], Hiroyuki Yoshida^{††}, and Mark Reagan[§]

*Departments of Anthropology and Pediatric Dentistry and [§]Department of Geology and Center for Global and Regional Environmental Research, The University of Iowa, Iowa City, IA 52242; [†]Institute of Archaeology, National Center for Social Sciences, Hanoi, Vietnam; [‡]Department of Anthropology, University of Massachusetts, Amherst, MA 01003; [¶]Quaternary Dating Research Centre, Research School of Pacific and Asian Studies, and ^{††}Research School of Chemistry, Australian National University, Canberra ACT 0200, Australia; [∥]National Museum of Natural History, P.O. Box 9517, 2300 RA Leiden, The Netherlands; and **Department of Physics and Astronomy, University of Calgary, Calgary AB T2N 1N4 Canada

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ABSTRACT Tham Khuyen Cave (Lang Son Province, northern Vietnam) is one of the more significant sites to yield fossil vertebrates in east Asia. During the mid-1960s, excavation in a suite of deposits produced important hominoid dental remains of middle Pleistocene age. We undertake more rigorous analyses of these sediments to understand the fluvial dynamics of Pleistocene cave infilling as they determine how skeletal elements accumulate within Tham Khuyen and other east Asian sites. Uranium/thorium series analysis of speleothems brackets the Pleistocene chronology for breaching, infilling, and exhuming the regional paleokarst. Clast analysis indicates sedimentary constituents, including hominoid teeth and cranial fragments, accumulated from very short distances and under low fluvial energy. Electron spin resonance analysis of vertebrate tooth enamel and sediments shows that the main fossil-bearing suite (S1-S3) was deposited about 475 thousand years ago. Among the hominoid teeth excavated from S1-S3, some represent Homo erectus and Gigantopithecus blacki. Criteria are defined to differentiate these teeth from more numerous Pongo pygmaeus elements. The dated cooccurrence of Homo erectus and Gigantopithecus blacki at Tham Khuyen helps to establish the long co-existence of these two species throughout east Asia during the Early and Middle Pleistocene.

Tham Khuyen Cave lies 125 km NNE of Hanoi and 30 km WSW of the Chinese border in Lang Son Province of northern Vietnam (Fig. 1a). A regional survey in 1964 identified the paleontological importance of the site (1), and excavations in 1965 recovered significant hominoid fossils (2-5). Tham Khuyen has become the best-known hominoid fossil site in Vietnam and one of the better-known in east Asia. In the west, Tham Khuyen is reputed for its geological association of Homo erectus and Gigantopithecus blacki teeth (6-8) and, more recently, for the taxonomic status of its small sample of orangutan teeth (9, 10). Despite 30 years of investigations, however, basic questions remain about the age of the deposits, the geological processes of sedimentary (and fossil) infilling, and the precise taxonomic attribution for many hominoid elements. We focus on these issues through two lines of investigation: (i) Studies of the Pleistocene fluvial dynamics for the Tham Khuyen locality suggest that the cave accumulated individual teeth through localized, low-energy fluvial and eluvial events. (ii) Electron spin resonance (ESR) analysis of vertebrate tooth enamel and sediments and uranium/thorium (U/Th) series analysis of speleothems indicate the age for the more important accumulations.

Sedimentary Dynamics

Karst hills and towers of Carboniferous limestones dominate the physiography of the province, with recessively eroded outcrops of intercalated sandstones also providing significant landscape features (Fig. 1). Tham Khuven Cave itself is situated 7 km SE of the administrative headquarters for Binh Gia District, a few hundred meters W of Lang Vech village, and some 20 m above the valley bottom. The cave contains infilled passages on two levels (6 m apart) with fossiliferous deposits confined to the upper level. The sedimentary nature of the upper level deposit is most evident in an area 10 m N of the cave entrance (Fig. 1c, right), where excavators identified a dark red, fossiliferous cave "breccia." In this section, we designate 17 sedimentological units representing three lithologies (Fig. 1c, right): a basal fluvial conglomerate (C1), 12 sandstone/siltstone units (S1-S12), and four travertine/siltstones (T1-T4) interbedded with S1-S12. Most units exhibit sharp erosional surfaces and variable degrees of calcite cementation. The sandy/silty fluvial conglomerate (C1) is present throughout the base of the section. Its clasts consist of well-rounded polycrystalline quartz, rounded-to-angular cemented cave sediment and soil (pebble-to-granule size), and phosphatic granules. Angular clasts, mostly quartz and sandstone, are also present (as granules-to-coarse sand) as are rare cobbles and boulders. Unit C1 was certainly deposited along the banks of a river that flowed through all passages in the present escarpment. Given this fluvial character, the silicates derive either from formations across the valley or from the paleodrainage of igneous basement rocks. Fine sediment (sand/silt matrix) and phosphatic grains derive from karst soils developed on slope deposits (including cave entrances) and the flood plain.

Units S1-S12 are mixtures of overbank deposits and materials eluviated from above the cave. Most clasts fall in the range of silt-to-sand, with minor though variable amounts of granules and pebbles, and very rare cobbles and boulders. Stringers and lenses of pebble conglomerates and granule-bearing sandstones and/or siltstones are common above some of the sharp discontinuities. Small laminated pockets and even crossbedded lenses are also present, particularly in unit S3. Clayey soil nodules appear in all units as do pebble-size clasts of calcite-cemented sediment reworked from pre-existing cemented cave deposits. Sediment color generally varies with calcite cementation. Poorly cemented sediments are yellowishred, while well-cemented sectors are brownish-yellow to pale yellow. Units S1-S3 form a homogeneous sedimentary suite that corresponds to the fossiliferous breccia of the original reports (1–5). The depositional environment for the suite must have been complex, but of lower energy levels than previously interpreted. The generally fine texture of the sediments suggests an alluvial regime of low velocity, with rare cobble and

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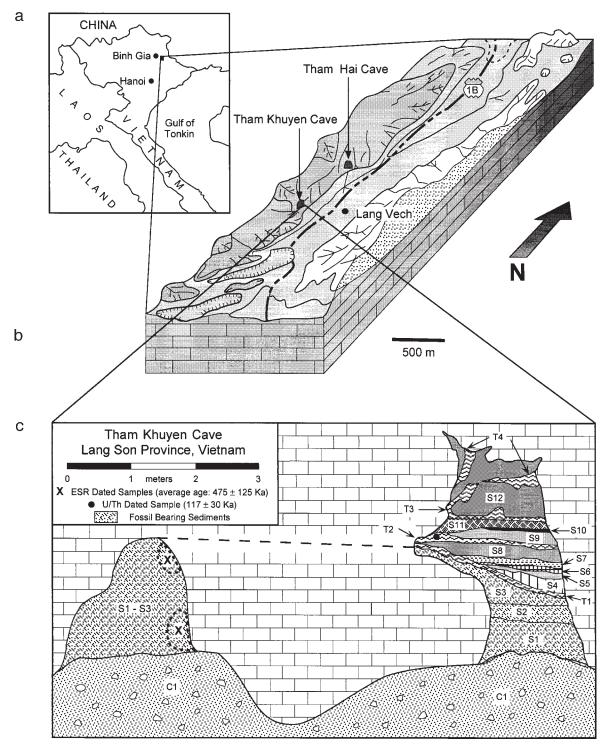


FIG. 1. Location, geomorphology, and stratigraphy of Tham Khuyen Cave. (a and b) The Tham Khuyen locality is defined by a large N–S valley whose flanks expose carbonates W (rising to 660 m), and silicates E (reaching 700 m). The valley contains an underfit stream (320 m) that meanders over thick clastic sediments to suggest a major river flowing S-to-N in the past. Caverns exposed along the W escarpment, such as Tham Khuyen, Tham Hai, and Keo Leng (3 km NW of Tham Khuyen), record three stages of Pleistocene evolution for an ancient karst system. The caves were once side passages within an underground drainage that was breached from above to form the present valley. The breached cavities were then infilled as the valley episodically choked with alluvium, and they were finally exhumed to produce the present paleokarst features. Dates discussed below indicate infilling proceeded at least from the middle Pleistocene. An interred stalagmite from Keo Leng (U/Th age range, 42 ka to 37 ka) suggests a very late Pleistocene transition from infilling to exhumation. (c) Frontal profile of Tham Khuyen Cave, N or right of main entrance. Stratigraphic section (right) lies 10 m N of cave entrance. Unit C1, sandy/silty fluvial conglomerate forms the basal infilling throughout the cave passages. Clasts consist of well-rounded polycrystalline quartz, rounded-to-angular cemented cave sediment and soil phosphatic granules, and rare sandstone cobbles and boulders. Fossiliferous units S1-S12 are mixtures of overbank deposits and materials eluviated from above the cave. Clasts range from silt to sand, with minor amounts of granules and pebbles and very rare sandstone cobbles and boulders. Travertines T1-T4 contain flowstone or cave pool deposits that indicate extended periods of nondeposition and consequent speleothem formation. Sedimentation in the cave was episodic as suggested by the sharp discontinuities between sediment units. Entrance to the intermediate tunnel (left) is located 5 m N of the cave entrance (5 m S of the main sediment outcrop and stratigraphic section). The tunnel is filled completely with highly fossiliferous sedimentary suite S1–S3. The ESR samples come from poorly cemented pockets of sediment within the tunnel.

larger-sized clasts incorporated as eluviation from within or above the cave. Significant in this regard is the calcitecemented sediment reworked from older infills into clasts. Given the high friability of this material, its preservation in clastic form indicates a nearby source as well as low-energy transport. Consequently, the fragmentary state of the fossil vertebrates must be explained by other than the immediate depositional environment (9).

Absolute Age. The "Stegodon-Ailuropoda fauna" at Tham Khuyen has always suggested an early to middle Pleistocene age for this deposit, and pollen analysis seems to corroborate (4, 5). ESR and U/Th series analyses increase the precision. ESR analyses address the S1-S3 suite as preserved within a small horizontal tunnel, intermediate between the cave entrance and the main sediment outcrop (Fig. 1c, left). Fifteen fossil teeth were extracted from poorly cemented sediment at two pocket-like sites within the tunnel. Procedures follow those of Grün (11-13), as presented in Table 1. The problem of ESR for dating tooth enamel lies in the uncertain U-uptake history for a given specimen, with early uptake (EU) and linear uptake (LU) alternatives (11, 12). Independent comparisons suggest that true age usually lies between the two models (15, 16). Age estimates are therefore computed for both models (average EU = 404 ± 51 ka; average $LU = 534 \pm 87$ ka) and averaged to give a general specimen estimate of 475 ± 125 ka. The four travertines contain significant amounts of flowstone/ dripstone and even calcite crystal arrays that normally form in still cave pools. Calcite crystals within a T2 speleothem are pure enough to analyze with U/Th methods, yielding an age estimate of 117 \pm 30 ka (1 σ), determined from a uranium concentration of 0.035 ± 0.004 ppm, 232-thorium not detectable $[(^{234}U)/(^{238}U) = 1.346 \pm 0.18, (^{230}Th)/(^{234}U) = 0.685 \pm$ 0.101)]. Unit T2 lies in the middle of the stratigraphic sequence, one travertine (T1) and 5 sandstone/siltstone units (S4–S8) above the S1–S3 suite (Fig. 1c, right). Consequently, the U/Th date for the T2 speleothem corroborates the average ESR date for the S1-S3 suite.

Hominoid Taxonomy

Hominoids comprise about 5% of approximately 2000 specimens of fossil vertebrates from Tham Khuyen Cave [faunal list (8)]. Most are isolated teeth recovered within the sedimentary suite S1-S3. Fragmentary condition complicates taxonomic assignment as, in considering each tooth a biological individual, the number of individuals multiplies immensely, thereby seeming to increase assemblage diversity. Understanding this effect, Vietnamese scientists are conservative in their species attributions, relating hominoid fossils to existing taxa (17-19). In the case of orangutan, for example, all teeth are assigned to the extant species Pongo pygmaeus. For Tham Khuyen, taxonomic problems lie rather in misidentification at the genus level, especially between Pongo and other hominoid genera. For example, large Pongo teeth have been termed Gigantopithecus while small worn Pongo teeth have been called Homo. Distinctions between Homo and Pongo molars are especially troublesome as they appeal to minor occlusal features that become less visible with wear as Franz Weidenreich saw nearly 60 years ago. Regarding occlusal wrinkling, Weidenreich observes that "there is no doubt that wrinkles represent a characteristic feature of the Sinanthropus molar and that they disappear gradually in the course of human evolution" (ref. 20, p. 103). Obviously, wrinkling becomes less diagnostic when comparing heavily worn molars of Homo. From the other side, Weidenreich cautions that even slightly worn upper molars of Pongo can occasionally exhibit "a pattern of the chewing surface surprisingly similar to that of Sinanthropus" (ref. 20, p. 66). In this same passage, nevertheless, Weidenreich identifies the distinguishing feature least sensitive to extreme wear: upper molars of Pongo uniquely exhibit a doubled crista

Table 1. Analytical data for teeth from Tham Khuyen and ESR age estimates

											Early U-uptake	uptake			Linear I	Linear U-uptake	
Sample	U(EN), ppm	U(DE), ppm	U(SED), ppm	Th(SED), ppm	$K(SED), \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \$	*Thickness, μm	*Removed, μ m	${\rm G}_{\rm B}^{\rm E}$	β -(SED), μ Gy/a	β -(DE), μ Gy/a	int. Ď, μGy/a	Total D, $\mu Gy/a$	Age, ka	eta-(DE), μ Gy/a	int. Ď, μGy/a	Total Ď, μGy/a	Age, ka
V78A	0.27 ± 0.03	26.1 ± 2.6	3.48 ± 0.28	12.45 ± 0.45	0.17 ± 0.05	3400 ± 300	100 ± 50	566 ± 21	64 ± 9	297 ± 43	140 ± 23	1449 ± 107	391 ± 32	141 ± 20	65 ± 11	1218 ± 98	465 ± 41
В	0.27 ± 0.03	27.3 ± 2.7	3.48 ± 0.28	12.45 ± 0.45	0.17 ± 0.05	3400 ± 300	100 ± 50	552 ± 36	64 ± 9	309 ± 45	139 ± 23	1460 ± 108	378 ± 37	146 ± 21	64 ± 12	1222 ± 98	451 ± 47
C	0.35 ± 0.04	26.8 ± 2.7	3.48 ± 0.28	12.45 ± 0.45	0.17 ± 0.05	3400 ± 300	100 ± 50	515 ± 55	64 ± 9	300 ± 43	179 ± 31	1491 ± 109	345 ± 45	142 ± 21	82 ± 16	1236 ± 99	417 ± 56
V79A	0.37 ± 0.04	45.4 ± 4.5	2.73 ± 0.57	12.83 ± 0.37	0.19 ± 0.05	1540 ± 100	180 ± 50	1043 ± 76	112 ± 16	999 ± 125	189 ± 32	2248 ± 161	464 ± 47	484 ± 62	90 ± 16	1634 ± 166	638 ± 65
В	0.83 ± 0.08	43.8 ± 4.4	2.73 ± 0.57	12.83 ± 0.37	0.19 ± 0.05	1540 ± 100	180 ± 50	1023 ± 55	112 ± 16	954 ± 121	418 ± 68	2432 ± 169	421 ± 37	463 ± 59	200 ± 33	1723 ± 118	594 ± 52
U	0.36 ± 0.04	45.5 ± 4.6	2.73 ± 0.57	12.83 ± 0.37	0.19 ± 0.05	1540 ± 100	180 ± 50	965 ± 37	112 ± 16	995 ± 126	182 ± 31	2237 ± 162	431 ± 35	482 ± 61	87 ± 15	1629 ± 115	592 ± 48
V80A	0.75 ± 0.08	26.5 ± 2.7	3.07 ± 0.50	13.70 ± 0.50	0.15 ± 0.05	4120 ± 300	500 ± 150	656 ± 32	34 ± 7	180 ± 35	402 ± 65	1564 ± 121	419 ± 38	86 ± 16	188 ± 32	1256 ± 102	522 ± 49
В	1.23 ± 0.12	24.9 ± 2.5	3.07 ± 0.50	13.70 ± 0.50	0.15 ± 0.05	3560 ± 300	250 ± 100	718 ± 35	50 ± 9	238 ± 41	640 ± 98	1876 ± 143	383 ± 35	115 ± 20	302 ± 48	1415 ± 109	507 ± 46
C	1.30 ± 0.13	23.5 ± 2.4	3.07 ± 0.50	13.70 ± 0.50	0.15 ± 0.05	4120 ± 300	500 ± 150	770 ± 28	34 ± 7	155 ± 31	694 ± 109	1831 ± 148	420 ± 37	75 ± 15	328 ± 52	1385 ± 110	556 ± 48
V81-1A	0.82 ± 0.08	33.3 ± 3.3	3.75 ± 0.10	14.70 ± 0.42	0.29 ± 0.05	1100 ± 150	100 ± 50	1288 ± 63	197 ± 25	967 ± 137	408 ± 68	$2520\pm\ 182$	511 ± 45	470 ± 67	196 ± 32	1811 ± 123	711 ± 60
В	0.95 ± 0.10	37.3 ± 3.7	3.75 ± 0.10	14.70 ± 0.42	0.29 ± 0.05	1100 ± 150	100 ± 50	1149 ± 97	197 ± 25	1067 ± 151	467 ± 79	2679 ± 197	429 ± 48	518 ± 74	224 ± 38	1887 ± 129	609 ± 66
V81–2A	0.26 ± 0.03	30.5 ± 3.1	2.43 ± 0.50	10.40 ± 0.10	0.13 ± 0.05	900 ± 150	50 ± 30	734 ± 41	144 ± 24	970 ± 138	119 ± 23	2181 ± 171	336 ± 32	466 ± 67	56 ± 11	1614 ± 119	455 ± 42
В	0.22 ± 0.02	32.0 ± 3.2	2.43 ± 0.50	10.40 ± 0.10	0.13 ± 0.05	900 ± 150	50 ± 30	702 ± 48	144 ± 24	1010 ± 142	102 ± 17	2204 ± 173	318 ± 33	485 ± 70	48 ± 8	1625 ± 121	431 ± 44
												Average	404 ± 51				534 ± 87
EN, e EN, e of the ex of ICP-N	mamel; DE, ive element: tternal β dos MS. Uncerta	dentine; Si s in the sed se rate acco ninties in th e dosimetry	ED, sedimer liment sampl ounts for a 5 ^c e elemental v bv A. Wies	EN, enamel; DE, dentine; SED, sediment; β -(), β dose rate; int., internal; D _E , dose; D, dose rate; γ -SED, 948 \pm 95 μ Gy/a. Uncertainty of the external γ dose rate consists of the variation of the radioactive elements in the sediment samples analyzed by NAA and ICP-MS, an average water concentration of 10.5%, and a possible systematic variation in the water content of 5%. The uncertainty of the external β dose rate accounts for a 5% variation of the past water concentration. The elemental analysis of U in enamel and dentine contains an estimated error of 10% for possible machine shifts of ICP-MS. Uncertainties in the elemental analysis of U elemental analysis of U in enamel and dentine contains an estimated error of 10% for possible machine shifts collbreted by a Maximum by a Wester (GSF, Munich). Calibration error of 2% is included in the D _e error estimation.	ose rate; int. by NAA and of the past wa re sediment (, internal; D ICP-MS, an ter concentr contain the c	al; D _E , dose; D, dose rate; γ-SED, 948 ± 95 μGy/a. Uncertainty of the external γ dose rate consists of the variation of the KS, an average water concentration of 10.5%, and a possible systematic variation in the water content of 5%. The uncertainty ncentration. The elemental analysis of U in enamel and dentine contains an estimated error of 10% for possible machine shifts a the differences between NAA and ICP-MS. *Thickness used to calculate β attenuation factors (14). The ⁶⁰ Co γ source was error of 2% is included in the D _m error estimation.	dose rate; tter concen slemental a between N.	γ -SED, 94 tration of 1 malysis of 1 AA and IC	$8 \pm 95 \ \mu G$ 10.5%, and a U in enamel PP-MS. *Thi	a possible and dentir ckness use	tainty of the systematic v ne contains a d to calcula	c external $\frac{1}{2}$ ariation in an estimate te β attenu	y dose rate the water	consists o content of 10% for po ors (14). T	of the variati 5%. The ur ossible mach he 60 Co γ so	on of the icertainty ine shifts ource was
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transversa, the mesial trigon crest uniting the paracone and protocone (ref. 20, p. 66). Peripheral placement of the molar cusps is another diagnostic feature of *Homo erectus* that stands out on all but the most worn specimens.

Homo and Gigantopithecus. Skeletal elements of Homo erectus are known from Zhoukoudian in northern China to Sangiran in eastern Java. This taxon was first identified at Tham Khuyen in 1967 by Khá and Bao (21) based on dental elements excavated in 1965. Khá and Cuong (22-24) later argued that as many as nine isolated specimens represent Homo erectus. Reanalysis of the Tham Khuyen dental sample confirms hominid status for five specimens [TK 65/50 (M¹), TK 65/53 (M¹), TK 65/105 (M²), TK 65/167 (C¹), and TK 65/8 (dm¹) (Fig. 2)] and demonstrates close affinities with equivalent teeth from Zhoukoudian. For the three upper molars, the human pattern of a single crista transversa and peripheral cusps is apparent. Occlusal morphology for these three is very similar to that for the upper molars from Zhoukoudian (ref. 20, plate 14, figures 119–120). In regard to metrics, crown areas (MD \times BL) for the two upper first molars (TK 65/50 = 151 and TK 65/53 = 161) fall within the range (117–162) for six equivalent teeth known from Zhoukoudian, and crown area for the second upper molar (TK 65/105 = 152) falls just above the range (129–149) for the seven equivalent Zhoukoudian specimens (ref. 20; table XVI). A similar pattern may be observed for the crown area of upper canine (TK 65/167 = 97) which falls within the range (83–109) of six upper canines from Zhoukoudian (ref. 20; table VII). There is general agreement that the deciduous molar TK 65/8 represents *Homo erectus*. However, four other teeth attributed to *Homo erectus* by Khá and Cuong (22–24) either fall outside the metric ranges for Zhoukoudian or lack diagnostic discrete features.

Fossil teeth of *Gigantopithecus blacki* are known from central and southern China, as far south as Daxin Cave, Guangxi Province (25). The identification of this taxon at Tham Khuyen Cave, first made by Khá and Long (26), extends the range 140 km SW. Lower left canine TK 65/122 (Fig. 2) can be attributed without doubt to *Gigantopithecus blacki*, based on comparisons with seven lower canines of *Giganto*-



FIG. 2. *Gigantopithecus blacki* canine (left) and *Homo erectus* molars (right) from Tham Khuyen. TK 65/122, left lower C of *Gigantopithecus blacki* (MD = 13.0, LL = 18.0, CH = 19.8), TK 65/105 (top right) left upper M2 (MD = 12.0, BL = 12.7), TK 65/50 (bottom right) left upper M1 (MD = 11.7, BL = 12.9). Scale bar is in cm. Other hominid teeth identified from Tham Khuyen include TK 65/53, a right upper M1 (MD = 12.1, BL = 13.3), TK 65/167 left upper C (MD = 9.9, LL = 9.8), and TK 65/8, a left upper deciduous M1 (MD = 9.9, BL = 10.8).

pithecus from China. For these canines Woo (27) calculates a shape index (LL \times 100 \div MD) with a range of 122–144 (table 19 in ref. 27). The index for TK 65/122 (= 139) falls squarely within the range of Gigantopithecus blacki. The lower canines of Chinese Gigantopithecus are very robust and low-crowned, with wear patterns distinct among the Hominoidea. The entire lingual surface (to the apex of the crown) gradually wears flat leaving the tooth wedge-shaped with a sharp cuting edge. TK 65/122 reveals this same unique morphological pattern. With regard to individual comparisons with the seven Gigantopithecus canines, TK 65/122 matches the morphology, wear stage, and overall size of PA 27 from Liucheng cave, Guangxi (plate 12 in ref. 27), one of the better preserved Gigantopithecus canines. One other specimen from Tham Khuyen, left lower incisor TK 65/146, may be attributed to Gigantopithecus blacki based on its buccal-lingual compression, peg-like morphology, and large size. However, joint reanalysis of three other teeth originally identified as Gigantopithecus [TK 65/61 (right upper central incisor), TK 65/124 (left lower incisor), and one other left incisor (un-numbered)], are now assigned to Pongo pygmaeus.

Discussion and Conclusion

Nominally we report the absolute ages for the more significant paleontological specimens from Tham Khuyen. We proceed an important step further, however, by linking the fossils and radiometric analysis with the sedimentary dynamics of the Tham Khuyen locality to reach two conclusions with implications. First, clast and U/Th series analyses show that while fluvial processes helped to accumulate skeletal fragments and individual teeth within the cave, other events and processes fragmented the elements prior to interment. We now must consider the role of scavengers in retrieving carcasses or bones from the locality and fragmenting them within the site. Scavenged bone accumulations play critical roles in the taphonomy of South African early hominid cave sites (28). East Asian sites such as Tham Khuyen certainly have bone accumulations as complex as their South African counterparts. Second, radiometric analyses of sediments and fossils suggest that Homo and Gigantopithecus co-occur at Tham Khuyen about a half million years ago. It is through this dated co-occurrence that we tie Tham Khuyen with larger issues of human evolution.

Homo and Gigantopithecus do co-occur at two other sites: Jianshi Cave, Hubei, China (29), and Longgupo Cave, Sichuan, China (30). Like Tham Khuyen, these localities may have accumulated the remains of open-dwelling fauna, not necessarily cave inhabitants. Thus, while each individual site holds evidence for co-occurrence, together they indicate that Homo and Gigantopithecus co-existed on a region-wide basis. Moreover, the two lineages shared a common range in east Asia for a very long period. We have recently dated the principal deposits at Longgupo Cave to more than 1.5 Ma, and perhaps to 1.9 Ma (30). With the Tham Khuyen co-occurrence of 475 ka, it is evident that Homo and Gigantopithecus co-existed for more than one million years. During this co-existence in Asia (throughout the early and middle Pleistocene), Gigantopithecus blacki increases in size but shows little morphological change while hominids undergo speciation. East Asian early hominids thus present two forms: a true Plio-Pleistocene Homo (species undetermined but with affinities to Homo ergaster and Homo habilis) at Longgupo (30) and middle Pleistocene Homo erectus, sensu stricto, at Tham Khuyen. It thus becomes clear that east and southeast Asia hold a very

long and complex sequence of Pleistocene human evolution, comparable, in fact, to that of East or South Africa. To push the intercontinental comparison further, given the diversity of their hominid samples as well as their scavenged, fluviatile bone accumulations, both Tham Khuyen and Longgupo are as complex as the South African cave sites. Our studies at Tham Khuyen demonstrate that the east Asian sites will become most important for understanding the totality of human evolution.

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