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## Geochronology and palaeoenvironments of Sibrambang and Djambu caves, western Sumatra

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### Abstract

Fossils from Sibrambang and Djambu, two sites in the Padang Highlands, were collected by Dubois in the late 1880s. These collections, alongside the deposits from Lida Ajer, have for over 100 years been our only insights into the Pleistocene mammalian history of Sumatra. Despite their importance, their chronological context has remained elusive. Here, we provide the first direct dates of fossils from Sibrambang and Djambu. Uranium–thorium series dating indicates that it is likely that the fossils from Djambu were derived from at least three periods: (1) >500 ka (beyond or close to the limit of the applied dating technique); (2) close to 85 ka (but not younger); and (3) close to 38 ka (but not younger). Sibrambang, too, has a mix of fossils with different ages, and it is hard to say how many distinct time intervals may be present. Conservatively, there are at least two: (1) >149 ka; and (2) >55 ka (but not younger than that). Stable carbon and oxygen isotope analyses of fossils from both sites indicate largely rainforest conditions during this period, except for one elephant specimen (>500 ka), which is reconstructed here as a mixed feeder. These data, combined with previous studies, hint at more open environments in Sumatra during (periods of) the Middle Pleistocene, although significantly more data will be required to confirm this. Our results have implications for previous palaeoecological analyses involving these sites, as well as for the taxonomy of fossil orangutan (*Pongo*).

*Keywords:* Pleistocene, rainforest, orangutan, carbon isotope, oxygen isotope

### Abstrak

Banyak fosil hasil koleksi Dubois pada tahun 1880-an dari dua lokasi di Dataran Tinggi Padang, Sibrambang dan Djambu. Dari koleksi tersebut, selain yang dikoleksi dari endapan gua Lida Ajer, selama lebih dari 100 tahun telah menjadi satu-satunya sumber wawasan kita dalam memahami

sejarah mamalia Pleistosen di pulau Sumatra. Terlepas dari pentingnya fosil tersebut, konteks kronologinya masih sulit untuk dipahami. Di sini, kami sampaikan hasil pertanggalan fosil-fosil dari Sibrambang dan Djambu menggunakan metode pertanggalan Uranium–Thorium. Pertanggalan deret U–Th menunjukkan bahwa setidaknya fosil-fosil dari Djambu setidaknya berasal dari tiga periode: (1) >500 ka (melampaui atau mendekati batas teknik pertanggalan yang diterapkan); (2) mendekati 85 ka (tetapi tidak lebih muda) dan (3) mendekati 38 ka (tetapi tidak lebih muda). Sibrambang juga memiliki campuran fosil dengan umur yang berbeda, sehingga menyulitkan untuk menyimpulkan berapa banyak interval umur yang berbeda yang mungkin ditemukan. Secara konservatif, setidaknya terdapat dua umur: (1) >149 ka; dan (2) yang lebih muda >55 ka (tetapi tidak lebih muda dari umur tersebut). Analisis isotop karbon dan oksigen stabil untuk fosil yang berasal dari kedua lokasi tersebut menunjukkan sebagian besar kondisi hutan hujan yang stabil selama periode ini, kecuali untuk satu spesimen gajah (>500 ka), yang di sini direkonstruksikan sebagai pemakan tumbuhan campuran. Data ini, dikombinasikan dengan data dari kajian-kajian sebelumnya mengisyaratkan lingkungan yang lebih terbuka di Sumatra selama periode Pleistosen Tengah, meskipun masih diperlukan lebih banyak data yang signifikan untuk mengkonfirmasi hal ini. Hasil kami telah memberikan implikasi pada analisis paleoekologi yang telah dilakukan sebelumnya yang melibatkan situs-situs tersebut, begitu pula dengan taksonomi fosil orangutan (*Pongo*).

*Kata kunci:* Plestosen, hutan hujan, orangutan, isotop karbon, isotop oksigen

## Introduction

In the late 1880s, Dubois began his search for the ‘missing link’ of human evolution in the Padang Highlands in western Sumatra. His exploration and excavation of several caves were initially met with a great deal of excitement, particularly for Lida Ajer (Dubois 1888). However, this excitement was eventually tempered and ultimately dampened when the only fossils recovered represented extant species from the region (Chapter 2, this volume). Dubois, and Hooijer after him, considered these to belong only to the Holocene (Dubois 1888; Hooijer 1947). Dubois moved his exploration to Java in 1890, leaving the bulk of the fossil materials from the Sumatran caves to be described by Hooijer in a series of papers (Hooijer 1946a, 1946b, 1947, 1948, 1955, 1960, 1962). Although Dubois collected from numerous caves in the Padang Highlands, the most substantial material he recovered was derived from only three caves: Lida Ajer, Sibrambang and Djambu.

The Sumatran cave deposits were attributed to the Holocene until the 1980s, when de Vos (1983) first pointed out the close faunal similarities between Punung in Java and Lida Ajer and Sibrambang in Sumatra and contrasted these with the sites of Wajak and Ngandong, also in Java. He observed that Punung I and II and the Sumatran caves sampled taxa reminiscent of interglacial humid forests and argued that they should be considered of similar antiquity and had been connected by a land bridge between Java and Sumatra. Ngandong and Wajak, on the other hand, represented drier habitats indicative of glacial periods. This, combined with biochronological data available at the time, suggested that Punung dated to sometime between Ngandong and Wajak. The contemporaneity of Punung, Lida Ajer and Sibrambang was subsequently accepted by some (e.g. Bacon et al. 2008; Janssen et al. 2016; Louys et al. 2007; Louys and Meijaard 2010).

The environmental context of the biocorrelations was an explicit and important aspect of the faunal turnover scheme proposed for determining the ages of Javanese Pleistocene sites (de Vos 1983, 1985, 1996; de Vos et al. 1994; Leinders et al. 1985; Sondaar 1984; van den Bergh et al. 2001). In this scheme, the more open woodlands represented by Middle Pleistocene sites such as

Trinil, Kedung Brubus and Ngandong gave way to interglacial rainforest conditions, as represented by the Late Pleistocene Punung I and II, only to be replaced by the more open Holocene sites of Sampung, Hoekgrot, Goa Jimbe and Wajak. Wajak is now understood to be Late Pleistocene (Storm et al. 2013).

Breccia from Punung III, a collapsed cave site found in the vicinity of Punung I and II and thought to be contemporaneous with them due to faunal similarities, was dated to between  $128 \pm 15$  and  $118 \pm 3$  ka using thermoluminescence (TL), optically stimulated luminescence, thermal ionisation mass spectrometry and uranium-series (U-series) dating (Westaway et al. 2007). This age range was subsequently applied to the Sumatran assemblages on biostratigraphic grounds (Janssen et al. 2016; Louys and Meijaard 2010; Louys et al. 2007), although some expressed caution regarding the implied relationship between Punung III and Punung I and II (Bacon et al. 2015; Kaifu et al. 2022).

The first attempt to directly date Sumatran material used amino-acid racemisation. Randy Skelton (pers. comm. cited in Drawhorn 1995) attempted to date a sample of bone from Lida Ajer and calibrated the racemisation using two dated samples collected from the deepest layers of the Niah Cave deposits in Borneo. Skelton observed that if racemisation rates between Niah and Lida Ajer were equivalent, then the Lida Ajer material would be older than 80,000 years. Skelton also dated two bone fragments from Djambu. These returned dates of 70–85 ka and 56 ka respectively, leading Drawhorn (1995) to suggest a minimum of 6,000–14,000 years of time averaging for the Djambu assemblage.

More recently, new exploration and sampling of caves in western Sumatra, specifically Lida Ajer, Ngalau Gupin and Ngalau Sampit, allowed for an evaluation of the age of fossil-bearing breccias in the Padang Highlands as well as several Dubois legacy fossils (Duval et al. 2021; Louys et al. 2022; Smith et al. 2021; Westaway et al. 2017). For Lida Ajer, red TL and post-infrared infrared-stimulated luminescence (pIR-IRSL) dating of the breccia sediments in the main fossil chamber provided burial ages of  $85 \pm 25$  ka and  $62 \pm 5$  ka respectively, with the latter probably closer to the true age of burial (Westaway et al. 2017). U-series dating of a basal flowstone to  $203 \pm 17$  ka provided a maximum age, while a straw stalactite derived from the breccia, dated to  $84 \pm 1$  ka, provided a probable true age of the deposit. Overlying flowstones, providing a minimum age, were dated to  $71 \pm 7$  ka and  $11 \pm 2$  ka.

Direct dating on a fossil orangutan tooth (*Pongo*) from the Dubois collection (Naturalis Biodiversity Centre, Leiden) using U-series dating produced a date of 70–60 ka. While this probably represents a minimum age for the fossil, this was not confirmed by Westaway et al. (2017). A similar age (>80–75 ka) was obtained by direct dating fossil teeth extracted directly from the breccia by Westaway et al. (2017), with the overall breccia deposit probably deposited between 63 and 73 ka (Westaway et al. 2017).

Louys et al. (2022) provided further details on the ages and stratigraphic relationship of the new recovered fossils from Lida Ajer, paying particular attention to the deposits from the passages at the rear of the cave. They combined electron spin resonance (ESR) dating of several teeth from unconsolidated muds, luminescence dating of non-fossiliferous sediments, and stratigraphic observations to construct a model of deposition history for the cave. Although the ‘sinkhole’ fossil deposits, topographically lower in the cave, are probably (but not conclusively) older than the material dated by Westaway et al. (2017), the most parsimonious interpretation of the history of the site suggests that all the fossils were deposited during Marine Isotope Stage (MIS) 4, corresponding to 76–59 ka, using the composite marine  $\delta^{18}\text{O}$  record provided by Westerhold et al. (2020). Stable

isotope analyses of the fossil teeth from Lida Ajer (both Dubois fossils and newly recovered fossils) indicated rainforest conditions similar to today, although potentially slightly wetter and with some small open patches (Louys et al. 2022).

Ngalau Sampit is one of the caves that also appear in Dubois' notes, although no specific fossils present in the Dubois collections have been associated with deposits from this cave (Duval et al. 2021). Exploration and initial U-series dating of flowstone and calcite by Louys et al. (2017), suggesting an age of approximately 90 ka for the deposit, were confirmed through a more comprehensive dating study by Duval et al. (2021). This latter study combined U-series/ESR ages of individual fossils (obtaining a mean age of  $105 \pm 9$  ka, 1 SD), and conducted breccia dating yielding internally  $1\sigma$ -consistent pIR-IRSL mean ages of  $93 \pm 6$  ka, 1 SD; it indicated deposition during MIS 5 (130–71 ka; Lisiecki and Raymo 2005). Thus, Ngalau Sampit is roughly coeval with Punung in Java. Although these sites have preserved relatively few fossil specimens, these specimens indicate that rainforest conditions were present in the Padang Highlands at that time (Louys et al. 2021).

Ngalau Gupin was first discovered during fieldwork in Padang Highlands in 2015 reported by Louys et al. (2017), and a detailed analysis of its fauna and age was described by Smith et al. (2021). The fauna is largely typical of already-known Pleistocene Sumatra, with the addition of several taxa not previously recorded from the fossils of the island, including the Indian rhinoceros (*Rhinoceros unicornis*) and the extinct Asian hippopotamus (*Hexaprotodon*). The fossils were recovered from cemented breccia and eroded material, with reconstructed ages between 160 and 115 ka based on combined U-series/ESR dating of teeth from the deposit. As such, the Ngalau Gupin fossils probably represent MIS 6 faunas (160–115 ka) and are currently the oldest directly dated remains from the region (Smith et al. 2021).

Here, we present the results of direct dating of Dubois legacy fossil teeth from Sibrambang and Djambu, complementing the renewed dating efforts at other sites in the Padang Highlands. We discuss the dates in the context of the probable depositional and taphonomic environment operating in these caves. We also present stable isotope analyses of the teeth from the three main cave sites and discuss these in the context of previous palaeoenvironmental and palaeoecological studies of the assemblages.

## Materials and methods

### Geographical context

Sibrambang (alternative spelling Simbrambang) is one of the most productive of Dubois' Sumatran cave localities. Dubois' notes suggest that material from this site was excavated from a cave called Agung Agung (Chapter 2, this volume). A cave bearing this name has been identified (but not yet explored) in the general vicinity of the modern village of Sibrambang (Louys et al. 2017). Drawhorn (1995) suggested that, given the importance of the cave site now known as Sibrambang, Dubois identified it not by the cave name but rather by the name of a nearby village or geological feature, and we argue it is likely that this village or feature name probably had one or two letters different from the site name and has been altered in transliteration to become Sibrambang. Djambu (original spelling Djamboe, modern alternative spelling Jambu) has better locality information recorded, although, like that of Sibrambang, its exact location remains to be determined. Dubois' notes indicate that the cave was located near and north of the Kulié-monies Volcano, west of the Muara-panas River, and at a relatively high altitude (Chapter 2, this volume, Appendix, 50-049) and north of the town of Tapisello.

## Material

From the Dubois material available from Sibrambang, two *Pongo*, one *Tapirus indicus*, two *Elephas maximus*, two *Capricornis sumatraensis* and six Rhinocerotidae enamel fragments were used as samples for carbon and oxygen isotope analysis, and the following teeth were dated: two *Pongo* (4 and 5 drill samples), one *Panthera pardus* (4 drill samples), one *Tapirus indicus* (4 drill samples) and one *Elephas maximus* (7 drill samples). From Dubois' Djambu collection, one *Capricornis sumatraensis*, three *Elephas maximus* and four Rhinocerotidae enamel fragments were used as samples for carbon and oxygen isotope analysis, and one *Pongo* tooth (5 drill holes), one *Tapirus indicus* tooth (4 drill holes), one *Panthera pardus* dental fragment (3 drill holes) and one *Elephas maximus* dental fragment (3 drill holes) were dated.

Each tooth or tooth fragment came from the bulk Dubois fossils housed at Naturalis Biodiversity Center, Leiden, the Netherlands. Bulk registration numbers for the fragments are listed in Tables 5.1 and 5.2 in the Results section. As each individual fragment listed under a bulk number did not have an individual registration number, we assigned each sample an internal number corresponding to the site they came from; samples were bagged with this number and returned to the bulk collections.

## Carbon and oxygen stable isotope analysis

Carbon and oxygen isotope analysis was undertaken on samples of powdered enamel obtained using a diamond burr drill bit applied to the exposed surface of the enamel. Enamel powder was treated chemically to remove organics using 30% H<sub>2</sub>O<sub>2</sub> and 0.1 N acetic acid. Samples were subsequently measured using a ThermoFinnigan DeltaPlus XP mass spectrometer at the University of Rochester's Stable Isotope Ratios in the Environment Analytical Laboratory. Carbon and oxygen isotopes are reported in permil (‰) and standardised to Vienna Pee-Dee Belemnite. Where sample size permitted, we ran repeat analyses. For these, we discarded the results with the highest standard deviation across both oxygen and carbon isotopes; where these were identical, the lower carbon standard deviation was retained.

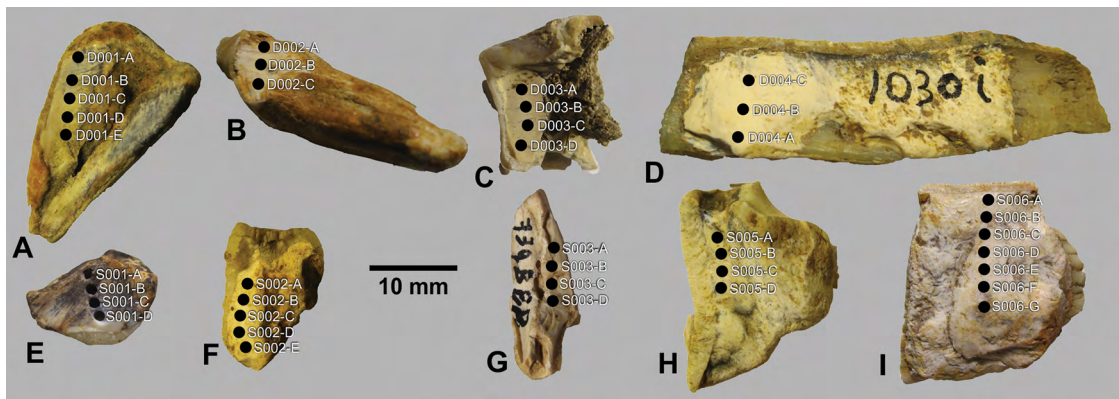
## U-series dating

Other than biochronology, geochronological methods applicable to the Djambu and Sibrambang fossil assemblages are limited to direct dating approaches. Because the caves have not been re-explored and sampled, stratigraphy-based geochronological methods are not currently applicable. Moreover, because the fossils are mostly isolated teeth that are well preserved but were prepared in a way that meant formerly adhering matrix was removed at the time of curation, luminescence and electron-based methods (which rely on knowledge of burial dose rates) are not possible. Hence, we were restricted to direct approaches such as uranium–thorium (U–Th) and radiocarbon dating. We chose the former because it is less destructive (a curatorial concern for the historic Dubois collections) than radiocarbon dating and has a far greater temporal application range (up to c. 500 ka versus c. 50 ka for radiocarbon dating).

Direct U–Th dating is based on the premise that vertebrate tissues such as teeth take up uranium (U) from the burial environment during the fossilisation process. <sup>238</sup>U then undergoes alpha and beta decay to produce a series of short-lived nuclides including <sup>234</sup>U, <sup>234</sup>Th and <sup>230</sup>Th (and eventually stable lead (Pb) daughter isotopes). The U–Th age is then calculated by measuring the ratio of the parent isotope, <sup>238</sup>U, to the daughter <sup>230</sup>Th. Because living tissues contain little or no U, direct U-series dating in most cases produces only minimum ages for the specimens, but in some situations, it can return dates that may approximate the true age (e.g. Price et al. 2021). Although teeth are open

systems for U uptake and migration, they may often act as closed systems after recrystallisation. In some cases, U may be lost from the system through leaching, leading to maximum ages (and age overestimates) for the fossils of concern (Sambridge et al. 2012). However, the reliability of the U-series age can be estimated by considering the geometry of  $^{230}\text{Th}$  age and U-concentration in a section (Pike et al. 2002).

We followed the sampling approach described in Price et al. (2013), which basically involved hand-drilling multiple dentine powders in transects across each tooth, with each sample then dated separately (see Figure 5.1). This approach allowed us to produce age and U-concentration profiles through the teeth and hence allows us to determine their suitability for U–Th dating. Again, to reduce the need to destructively sample the teeth—for example, by cut and slabbing as would be required for U–Th laser ablation approaches (e.g. Grün et al. 2014)—our hand-drilling utilised drill bits of only 1 mm diameter (producing c. 1 mg of dentine powder per sample) and targeted already-broken and naturally exposed dentine surfaces. The sample powders were measured on a Nu Plasma HR multi-collector inductively coupled plasma mass spectrometer following techniques described in Zhou et al. (2011) using the infrastructure in the Radiogenic Isotope Facility at The University of Queensland, Brisbane, Australia.



**Figure 5.1: The nine dated teeth from the Dubois collections from Sibrambang and Djambu, showing sampling positions.**

Note: See Table 5.2 for the results.

- A. D001 (*Pongo* sp., Djambu).
- B. D002 (*Panthera pardus*, Djambu).
- C. D003 (*Tapirus indicus*, Djambu).
- D. D004 (*Elephas maximus*, Djambu).
- E. S001 (*Pongo* sp., Sibrambang).
- F. S002 (*Pongo* sp., Sibrambang).
- G. S003 (*Panthera pardus*, Sibrambang).
- H. S005 (*Tapirus indicus*, Sibrambang).
- I. S006 (*Elephas maximus*, Sibrambang).

Source: Image by G.J. Price.

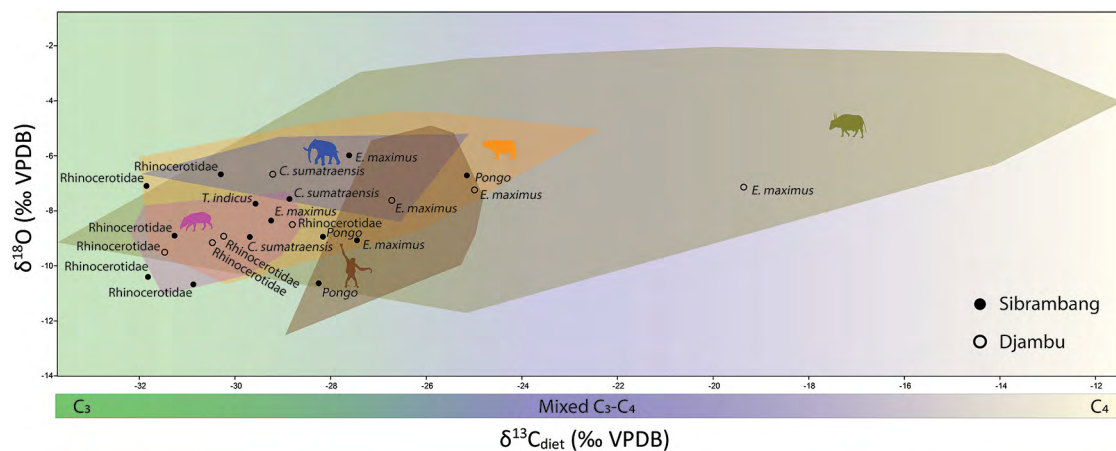


## Results

### Stable isotopes

The carbon and oxygen isotope values are listed in Table 5.1. Elephants demonstrated the largest range of carbon isotope values, with a large  $C_4$  contribution to diet in one individual from Djambu (Figure 5.2). However, all other elephant samples showed a carbon isotope either dominated by or having a large proportion of  $C_3$ . All the other taxa examined had carbon isotope values well towards or in the  $C_3$  range, with rhinoceroses exhibiting the lowest  $\delta^{13}C$  values of any of the sampled specimens.

Oxygen isotopes were all highly negative, as would be expected from a humid or rainforest environment. An elephant specimen from Sibrambang had the highest value, at  $-6\text{‰}$   $\delta^{18}O$ , while a rhinoceros specimen from this site had the lowest value, at  $-10.7\text{‰}$   $\delta^{18}O$ . The  $C_4$ -eating elephant had oxygen isotope ratios within the range of all the other elephants examined, and only one  $C_3$  elephant had lower  $\delta^{18}O$  values than modern elephants.



**Figure 5.2: Stable isotope analysis of  $\delta^{13}C_{\text{diet}}$  (‰ VPDB) and  $\delta^{18}O$  (‰ VPDB) from faunal enamel of fossil mammals collected by Dubois from Sibrambang and Djambu compared with modern Southeast Asian representatives of their families.**

Note: Modern representatives' data are shown as convex hulls; see Louys and Roberts (2020) for original data. Pink: Tapiridae; blue: Elephantidae; brown: Hominidae (*Pongo*); orange: Rhinocerotidae; green: Bovidae. *E. maximus* = *Elephas maximus*; *T. indicus* = *Tapirus indicus*; *C. sumatraensis* = *Capricornis sumatraensis*.

VPDB = Vienna Pee-Dee Belemnite.

Source: Image by J. Louys using animal silhouettes from phylopic.org (public domain) and CC-BY-SA 3.0. All animal silhouettes via phylopic.org: *Pongo abelii* by Gareth Monger (creativecommons.org/licenses/by/3.0/); *Mammuthus armeniacus* by Julián Bayona (creativecommons.org/licenses/by-nc/3.0/); *Tapirus pinchaque* by Steven Traver (creativecommons.org/publicdomain/zero/1.0/); *Bubalus arnee* by Cristopher Silva (creativecommons.org/publicdomain/zero/1.0/); *Rhinoceros unicornis* by H.F.O March (creativecommons.org/publicdomain/mark/1.0/). CC-BY-NC 3.0 Elephantini by Zimices.

**Table 5.1: Carbon and oxygen isotope analysis values calculated for select taxa from Dubois' collections from Sibrambang and Djambu.**

Site	Collection no.	Internal sample ID	Taxon	Common name	Carbon, $\delta^{13}\text{C}_{\text{diet}}$		Oxygen, $\delta^{18}\text{O}$	
					mean ‰ VPDB	SD	mean ‰ VPDB	SD
Djambu	1030i	D004	<i>Elephas maximus</i>	Asian elephant	-5.36	0.05	-7.14	0.10
Djambu	959aan	D005	<i>Capricornis sumatraensis</i>	Mainland serow	-15.21	0.05	-6.67	0.13
Djambu	1030i	D008	<i>E. maximus</i>	Asian elephant	-12.72	0.08	-7.62	0.10
Djambu	1030i	D009	<i>E. maximus</i>	Asian elephant	-10.99	0.05	-7.24	0.11
Djambu	1022a	D010	<i>Rhinocerotidae</i>	Rhinoceros	-17.46	0.05	-9.51	0.21
Djambu	1022a	D011	<i>Rhinocerotidae</i>	Rhinoceros	-16.48	0.07	-9.14	0.14
Djambu	1022a	D012	<i>Rhinocerotidae</i>	Rhinoceros	-16.23	0.05	-8.93	0.11
Djambu	1022a	D013	<i>Rhinocerotidae</i>	Rhinoceros	-14.8	0.1	-8.50	0.13
Sibrambang	739au	S001	<i>Pongo</i> sp.	Orangutan	-17.16	0.09	-8.95	0.16
Sibrambang	810q	S002	<i>P. pygmaeus</i>	Orangutan	-14.15	0.05	-6.70	0.20
Sibrambang	815g	S005	<i>Tapirus indicus</i>	Malayan tapir	-15.57	0.05	-7.74	0.10
Sibrambang	7989a	S006	<i>E. maximus</i>	Asian elephant	-13.44	0.06	-9.05	0.11
Sibrambang	810n	S007	<i>E. maximus</i>	Asian elephant	-13.6	0.06	-5.98	0.10
Sibrambang	961t	S008	<i>C. sumatraensis</i>	Mainland serow	-15.69	0.03	-8.94	0.09
Sibrambang	961s	S009	<i>C. sumatraensis</i>	Mainland serow	-14.87	0.08	-7.57	0.14
Sibrambang	809	S012	<i>E. maximus</i>	Asian elephant	-15.24	0.06	-8.35	0.14
Sibrambang	971aa	S013	<i>Rhinocerotidae</i>	Rhinoceros	-16.87	0.07	-10.65	0.11
Sibrambang	971aa	S014	<i>Rhinocerotidae</i>	Rhinoceros	-17.24	0.06	-8.93	0.21
Sibrambang	971aa	S015	<i>Rhinocerotidae</i>	Rhinoceros	-16.32	0.06	-6.66	0.09
Sibrambang	971aa	S016	<i>Rhinocerotidae</i>	Rhinoceros	-17.85	0.07	-7.11	0.13

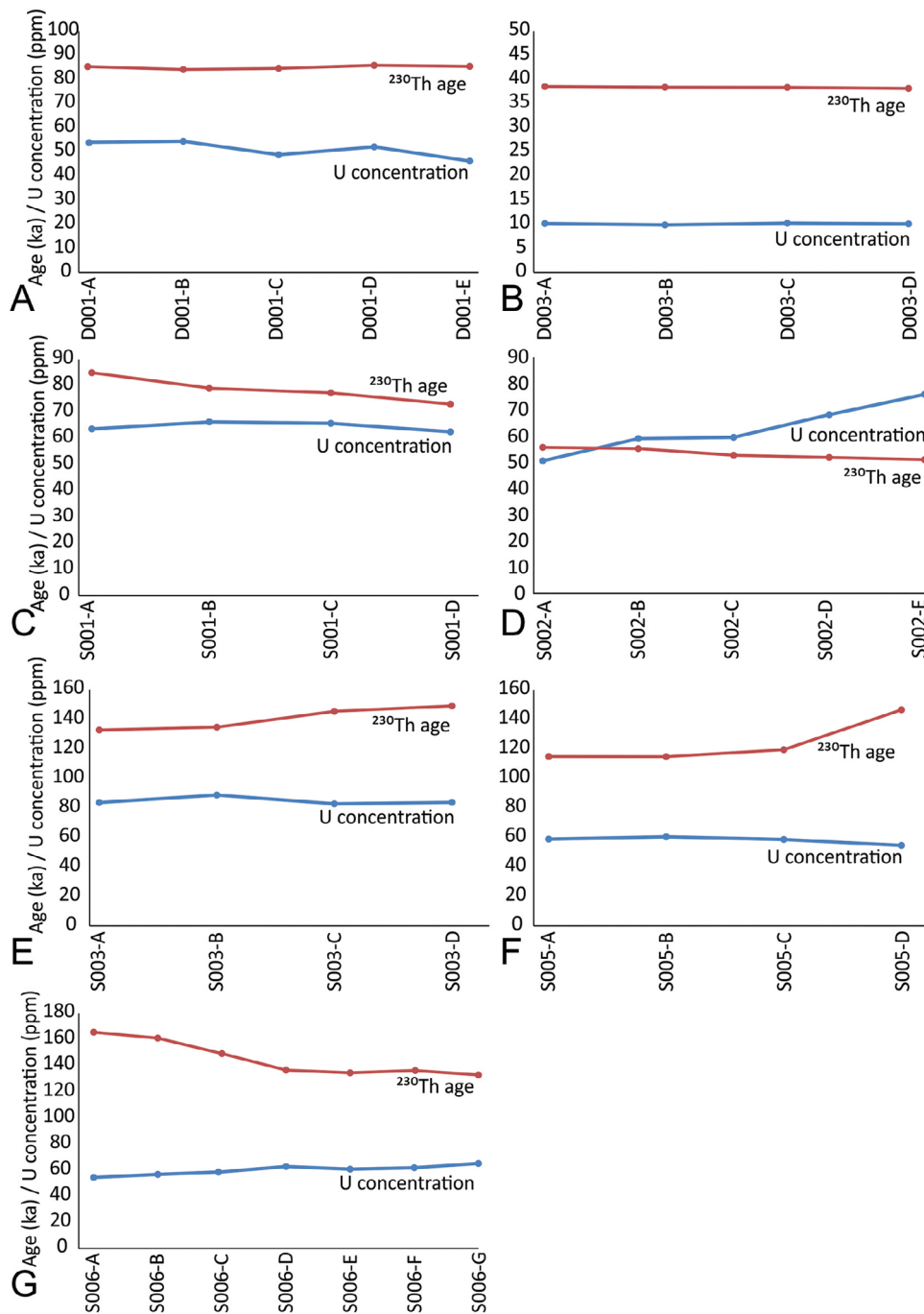
Note: VPDB = Vienna Pee-Dee Belemnite.

Source: Data from the authors.

## U–Th dating

We produced a total of 40 U–Th dates for nine fossil teeth (four from Djambu and five from Sibrambang) and included specimens referable to *Pongo* sp., *Tapirus indicus*, *Panthera pardus* and *Elephas maximus* (see Figure 5.3 and Table 5.2). Although the dating of each dentine sample was relatively straightforward, interpretation was more challenging due to the apparent variable nature of U uptake and loss in the teeth; this complicated the interpretation of the respective assemblages.





**Figure 5.3:**  $^{230}\text{Th}$  age and U-concentration profiles in sections of dated fossil teeth from Dubois' collections from Sibrambang and Djambu.

Note: Specimens that exhibited clear U loss – D002 and D004 – are not plotted. See Table 5.2 for specific isotopic data for all teeth (including D002 and D004).

- |   |   |   |
|---|---|---|
| A. D001 ( <i>Pongo</i> sp., Djambu).        | E. S003 ( <i>Panthera pardus</i> , Sibrambang). | G. S006 ( <i>Elephas maximus</i> , Sibrambang). |
| B. D003 ( <i>Tapirus indicus</i> , Djambu). |   |   |
| C. S001 ( <i>Pongo</i> sp., Sibrambang).    | F. S005 ( <i>Tapirus indicus</i> , Sibrambang). |   |
| D. S002 ( <i>Pongo</i> sp., Sibrambang).    |   |   |

Source: Image by G.J. Price.

Table 5.2: Uranium-series isotopic and concentration data for fossil teeth from Dubois' collections from Sibrambang and Djambu.

Sample name'	Collection no.	Taxon	U (ppm)	<sup>232</sup> Th (ppb)	<sup>230</sup> Th/ <sup>232</sup> Th	<sup>230</sup> Th/ <sup>238</sup> U	<sup>234</sup> U/ <sup>238</sup> U	Uncorrected age (ka)	Corrected age (ka)	Corrected initial ( <sup>234</sup> U/ <sup>238</sup> U)
D001-A	937d	<i>Pongo</i> sp.	53.94 ± 0.03	7.48 ± 0.10	14383	0.657 ± 0.003	1.190 ± 0.001	85.3 ± 0.6	85.3 ± 0.6	1.2417 ± 0.0013
D001-B	937d	<i>Pongo</i> sp.	54.35 ± 0.03	4.85 ± 0.09	22197	0.653 ± 0.003	1.193 ± 0.001	84.1 ± 0.5	84.1 ± 0.5	1.2451 ± 0.0016
D001-C	937d	<i>Pongo</i> sp.	48.76 ± 0.02	1.18 ± 0.03	82095	0.654 ± 0.002	1.191 ± 0.002	84.5 ± 0.4	84.5 ± 0.4	1.2427 ± 0.0018
D001-D	937d	<i>Pongo</i> sp.	52.08 ± 0.03	2.34 ± 0.05	44394	0.658 ± 0.002	1.188 ± 0.001	85.8 ± 0.4	85.8 ± 0.4	1.2389 ± 0.0010
D001-E	937d	<i>Pongo</i> sp.	46.23 ± 0.02	1.80 ± 0.04	50750	0.652 ± 0.002	1.181 ± 0.001	85.3 ± 0.5	85.3 ± 0.5	1.2300 ± 0.0012
D002-A	937b	<i>Panthera pardus</i>	37.53 ± 0.03	1.80 ± 0.05	81298	1.286 ± 0.003	1.218 ± 0.001	473.6 ± 17.1	473.6 ± 17.1	1.8286 ± 0.0387
D002-B	937b	<i>P. pardus</i>	34.15 ± 0.02	503.78 ± 1.17	277	1.345 ± 0.004	1.217 ± 0.001	>500	>500	
D002-C	937b	<i>P. pardus</i>	37.79 ± 0.01	39.67 ± 0.11	3833	1.326 ± 0.004	1.228 ± 0.001	746.0 ± 137.7	746.0 ± 137.7	2.8761 ± 0.7253
D003-A	10061	<i>Tapirus indicus</i>	10.16 ± 0.01	65.16 ± 0.17	161	0.339 ± 0.003	1.129 ± 0.001	38.7 ± 0.5	38.5 ± 0.5	1.1441 ± 0.0014
D003-B	10061	<i>T. indicus</i>	9.87 ± 0.01	13.91 ± 0.03	727	0.338 ± 0.001	1.131 ± 0.001	38.4 ± 0.2	38.4 ± 0.2	1.1466 ± 0.0016
D003-C	10061	<i>T. indicus</i>	10.26 ± 0.01	4.32 ± 0.02	2430	0.337 ± 0.002	1.131 ± 0.001	38.3 ± 0.2	38.3 ± 0.2	1.1458 ± 0.0014
D003-D	10061	<i>T. indicus</i>	10.10 ± 0.01	8.46 ± 0.05	1214	0.335 ± 0.002	1.129 ± 0.002	38.1 ± 0.3	38.1 ± 0.3	1.1438 ± 0.0019
D004-A	1030i	<i>Elephas maximus</i>	7.594 ± 0.002	12.12 ± 0.03	2872	1.511 ± 0.005	1.361 ± 0.002	659.7 ± 73.1	659.7 ± 73.1	3.3232 ± 0.4748
D004-B	1030i	<i>E. maximus</i>	7.658 ± 0.004	25.64 ± 0.08	1464	1.615 ± 0.004	1.359 ± 0.001	>500	>500	
D004-C	1030i	<i>E. maximus</i>	7.846 ± 0.004	16.62 ± 0.04	2259	1.578 ± 0.006	1.349 ± 0.001	>500	>500	

Sample name <sup>1</sup>	Collection no.	Taxon	U (ppm)	<sup>232</sup> Th (ppb)	<sup>230</sup> Th/ <sup>232</sup> Th	<sup>230</sup> Th/ <sup>238</sup> U	<sup>234</sup> U/ <sup>238</sup> U	Uncorrected age (ka)	Corrected age (ka)	Corrected initial ( <sup>234</sup> U/ <sup>238</sup> U)
D004-D	1030i	<i>E. maximus</i>	7.135 ± 0.002	111.94 ± 0.23	301	1.554 ± 0.004	1.350 ± 0.001	>500	>500	
S001-A	739au	<i>Pongo</i> sp.	63.52 ± 0.03	4.70 ± 0.10	26068	0.636 ± 0.002	1.157 ± 0.001	84.9 ± 0.5	84.9 ± 0.5	1.1993 ± 0.0011
S001-B	739au	<i>Pongo</i> sp.	66.24 ± 0.06	11.34 ± 0.07	10710	0.604 ± 0.002	1.156 ± 0.001	79.0 ± 0.5	79.0 ± 0.5	1.1946 ± 0.0010
S001-C	739au	<i>Pongo</i> sp.	65.69 ± 0.03	9.46 ± 0.09	12530	0.595 ± 0.002	1.156 ± 0.001	77.3 ± 0.4	77.3 ± 0.4	1.1937 ± 0.0012
S001-D	739au	<i>Pongo</i> sp.	62.43 ± 0.02	9.30 ± 0.06	11588	0.569 ± 0.002	1.151 ± 0.001	73.0 ± 0.3	73.0 ± 0.3	1.1856 ± 0.0015
S002-A	810q	<i>Pongo</i> sp.	51.26 ± 0.03	9.78 ± 0.07	7311	0.460 ± 0.002	1.129 ± 0.001	56.4 ± 0.3	56.4 ± 0.3	1.1514 ± 0.0010
S002-B	810q	<i>Pongo</i> sp.	59.75 ± 0.03	3.28 ± 0.06	25108	0.454 ± 0.002	1.122 ± 0.001	55.9 ± 0.3	55.9 ± 0.3	1.1429 ± 0.0010
S002-C	810q	<i>Pongo</i> sp.	60.24 ± 0.05	4.61 ± 0.10	17367	0.438 ± 0.002	1.122 ± 0.001	53.4 ± 0.3	53.4 ± 0.3	1.1419 ± 0.0011
S002-D	810q	<i>Pongo</i> sp.	68.83 ± 0.04	3.08 ± 0.07	29333	0.433 ± 0.002	1.123 ± 0.001	52.6 ± 0.3	52.6 ± 0.3	1.1426 ± 0.0012
S002-E	810q	<i>Pongo</i> sp.	76.59 ± 0.04	10.18 ± 0.14	9750	0.427 ± 0.002	1.121 ± 0.001	51.8 ± 0.3	51.8 ± 0.3	1.1401 ± 0.0009
S003-A	739bbd	<i>P. pardus</i>	83.62 ± 0.06	3.11 ± 0.10	67568	0.828 ± 0.003	1.151 ± 0.001	132.7 ± 0.8	132.7 ± 0.8	1.2196 ± 0.0014
S003-B	739bbd	<i>P. pardus</i>	88.62 ± 0.10	6.43 ± 0.13	34803	0.832 ± 0.003	1.148 ± 0.001	134.7 ± 0.9	134.7 ± 0.9	1.2166 ± 0.0015
S003-C	739bbd	<i>P. pardus</i>	82.66 ± 0.09	21.36 ± 0.16	10120	0.862 ± 0.003	1.144 ± 0.001	145.4 ± 1.2	145.4 ± 1.2	1.2170 ± 0.0018
S003-D	739bbd	<i>P. pardus</i>	83.68 ± 0.06	5.24 ± 0.11	41770	0.862 ± 0.003	1.132 ± 0.001	149.0 ± 1.0	149.0 ± 1.0	1.2017 ± 0.0018
S005-A	815g	<i>T. indicus</i>	60.16 ± 0.04	15.05 ± 0.10	9701	0.800 ± 0.003	1.192 ± 0.001	116.1 ± 0.9	116.1 ± 0.7	1.2667 ± 0.0012
S005-B	815g	<i>T. indicus</i>	61.73 ± 0.06	7.27 ± 0.11	20522	0.797 ± 0.002	1.188 ± 0.001	116.0 ± 0.6	116.0 ± 0.6	1.2613 ± 0.0016

Sample name <sup>1</sup>	Collection no.	Taxon	U (ppm)	<sup>232</sup> Th (ppb)	<sup>230</sup> Th/ <sup>232</sup> Th	<sup>230</sup> Th/ <sup>238</sup> U	<sup>234</sup> U/ <sup>238</sup> U	Uncorrected age (ka)	Corrected age (ka)	Corrected initial ( <sup>234</sup> U/ <sup>238</sup> U)
S005-C	815g	<i>T. indicus</i>	59.87 ± 0.03	4.87 ± 0.08	30593	0.820 ± 0.003	1.194 ± 0.001	120.7 ± 0.9	120.7 ± 0.9	1.2730 ± 0.0015
S005-D	815g	<i>T. indicus</i>	55.90 ± 0.02	16.30 ± 0.09	9529	0.916 ± 0.003	1.197 ± 0.001	147.8 ± 0.9	147.8 ± 0.9	1.2994 ± 0.0018
S006-A	7989a	<i>E. maximus</i>	54.33 ± 0.04	29.01 ± 0.09	5345	0.941 ± 0.003	1.170 ± 0.001	165.6 ± 1.1	165.6 ± 1.1	1.2712 ± 0.0015
S006-B	7989a	<i>E. maximus</i>	56.67 ± 0.04	24.12 ± 0.08	6616	0.928 ± 0.004	1.170 ± 0.002	161.0 ± 1.5	161.0 ± 1.5	1.2670 ± 0.0023
S006-C	7989a	<i>E. maximus</i>	58.65 ± 0.04	21.47 ± 0.09	7401	0.893 ± 0.003	1.167 ± 0.0001	149.2 ± 1.2	149.2 ± 1.2	1.2541 ± 0.0018
S006-D	7989a	<i>E. maximus</i>	62.68 ± 0.03	12.20 ± 0.09	13248	0.850 ± 0.004	1.162 ± 0.001	136.5 ± 1.1	136.5 ± 1.1	1.2382 ± 0.0016
S006-E	7989a	<i>E. maximus</i>	60.61 ± 0.04	2.08 ± 0.07	74368	0.842 ± 0.003	1.161 ± 0.002	134.4 ± 1.0	134.4 ± 1.0	1.2351 ± 0.0024
S006-F	7989a	<i>E. maximus</i>	61.74 ± 0.04	2.77 ± 0.11	57476	0.850 ± 0.003	1.164 ± 0.001	136.2 ± 0.9	136.2 ± 0.9	1.2409 ± 0.0017
S006-G	7989a	<i>E. maximus</i>	64.99 ± 0.04	30.98 ± 0.12	5321	0.836 ± 0.003	1.160 ± 0.001	132.8 ± 0.9	132.8 ± 0.9	1.2327 ± 0.0017

<sup>1</sup> D = Djambu; S = Sibrambang.

Note: There is evidence of U leaching in D002 and D004; thus, <sup>230</sup>Th ages could not be calculated for all subsamples.

Ratios in parentheses are activity ratios calculated from the atomic ratios but normalised to measured values of secular-equilibrium HU-1 (Ludwig et al. 1992). Errors are given at the 2σ level. <sup>230</sup>Th ages were calculated using isoplot EX 3.0 (Ludwig 2003) with decay constants λ<sub>238</sub>U = 1.551 × 10<sup>-10</sup> yr<sup>-1</sup> for <sup>238</sup>U, λ<sub>234</sub>U = 2.826 × 10<sup>-6</sup> yr<sup>-1</sup> for <sup>234</sup>U and λ<sub>230</sub>Th = 9.158 × 10<sup>-6</sup> yr<sup>-1</sup> for <sup>230</sup>Th (Cheng et al. 2000). 2σ errors in the uncorrected ages were propagated directly from the uncertainties in (<sup>230</sup>Th/<sup>238</sup>U) and (<sup>234</sup>U/<sup>238</sup>U). The corrected <sup>230</sup>Th age was calculated using an assumed bulk earth or upper crust value equivalent to a detrital <sup>230</sup>Th/<sup>232</sup>Th activity ratio of 0.83.

Source: Data from the authors.

As shown in Figure 5.3, dating of the Djambu samples revealed two specimens with plateau-like  $^{230}\text{Th}$  age and U-concentration profiles: D001 (*Pongo* sp.) and D003 (*T. indicus*). This suggests relatively rapid uranium uptake following burial, without subsequent leaching. Thus, these two teeth represent reliable minimum ages that may be close to the true age of these specimens. These are c. 85 ka and c. 38 ka respectively. Samples D002 (*P. pardus*) and D004 (*E. maximus*) are less ideal for constraining the age of Djambu. Both show some evidence of uranium loss and are probably older than 500 ka and therefore beyond the applicable temporal range of the U–Th method. Collectively, these results suggest that the curated Djambu fossil collection may be significantly time-averaged. Given the lack of stratigraphic context recorded by Dubois and his team, it is possible that the teeth were reworked into a single stratigraphic layer prior to excavation or were collected from three separate and variously aged strata (i.e. c. 38 ka, c. 85 ka, and >500 ka). We consider the latter to perhaps be a slightly more parsimonious interpretation, given the lack of evidence of abrasion (which would indicate transport or reworking) on the fossils, and the fact that it is not uncommon for other caves in the Padang Highlands to contain stratigraphically complex and temporally various deposits (e.g. Louys et al. 2022; Smith et al. 2021).

U-migration behaviour in dated specimens from the Sibrambang assemblage is slightly different from that of Djambu. While there is no strong evidence for U loss in any of the teeth, there are no plateau-like  $^{230}\text{Th}$  age profiles either. The evidently youngest specimen, S002 (*Pongo* sp.), has a half- $\cap$ -shaped age profile where the  $^{230}\text{Th}$  ages become progressively older from the outer margin of the tooth to the inner portion but with an inverse relationship with regard to U-concentration; that is, the highest U-concentration is closest to the outer margin (note that this tooth was only drilled for dateable samples from the outer margin to the middle rather than completely across the tooth, outer margin to outer margin). This profile resembles a tooth that has experienced more recent U uptake, without U loss (e.g. Pike et al. 2002). The tooth yields a reliable minimum age of >56 ka (i.e. from subsample S002-A, closest to the middle of the specimen), although we cannot be sure how close this may be to the true age of the fossil. Sample S001 (*Pongo* sp.) has a similar profile to S002 and is >85 ka; likewise, we also interpret that to be a reliable minimum age. Three specimens (S003, *P. pardus*; S005, *T. indicus*; S006, *E. maximus*) have half-U-shaped  $^{230}\text{Th}$  age profiles in which the oldest ages occur towards the outer margin of the tooth and are progressively younger interiorward. Due to the relatively plateau-like U-concentration profiles through the teeth, there is no evidence for U loss, and thus these three teeth yield reliable minimum ages. Perhaps noteworthy, these teeth all have late Middle Pleistocene minimal ages (S003 and S005 >148 ka; S006 >165 ka; see Table 5.2). Again, it is challenging to draw firm conclusions about the overall age of the complete Sibrambang assemblage, but it remains possible that multiple and/or temporally various strata were sampled during the Dubois excavations. The clustering of at least three Sibrambang teeth with evidently similar U-uptake histories and minimum ages may show that those particular specimens were excavated from a single stratum.

## Discussion

The new dates produced here are useful in reconstructing, as a first approximation, both the time depth and likely time averaging present in the deposits of Sibrambang and Djambu. These new dates help place Dubois' sites in a regional geochronological framework and provide direct minimum ages for several taxa in the Padang Highlands. Both sites preserve orangutan fossils with minimum ages of around 85 ka, with the uptake interpretation suggesting this could be close to their true ages. Orangutan fossils are recorded from Ngatau Sampit (c. 100 ka; Duval et al. 2021), Ngatau Gupin (c. 160–115 ka; Smith et al. 2021) and the later Lida Ajer deposits (Westaway

et al. 2017), so their presence elsewhere in the Padang Highlands at c. 85 ka is to be expected. The minimum age of c. 50 ka for *Pongo* from Sibrambang may indicate persistence of this taxon after the Lida Ajer deposits; however, such interpretations require further testing and analysis. A conservative interpretation would suggest an older age for this specimen.

The *P. pardus* dating records suggest that leopards lived in the Padang Highlands from at least 148 ka. Meijaard (2004) hypothesised that the leopard first migrated into Sundaland in the Middle Pleistocene. Our data would appear to support this hypothesis; moreover, given the presence of these fossils, it is evident that this taxon did not bypass Sumatra on its way to Java.

Of course, the leopard is no longer found on the island of Sumatra, and several hypotheses have been proposed regarding its absence. Meijaard (2004) suggested that the prey densities that could be supported by the evergreen rainforests of Borneo and Sumatra were too low to sustain leopards in competition with tigers. Wilting et al. (2012, 2016) strongly advocated that the Toba eruption (c. 74 ka) was the primary cause of the leopard's extinction. Wilkinson and O'Regan (2003) suggested that life history traits, specifically the leopard's smaller litter size and shorter reproductive life relative to the tiger, were key factors explaining the absence of leopards on Indonesian islands such as Sumatra. Volmer et al. (2017) used agent-based modelling to examine the extinction of the leopard on Sumatra, concluding that the leopard could have been driven to extinction by competition from other carnivores, specifically from two medium-sized cats and the Asiatic wild dog. Our data indicates that the leopard persisted on Sumatra from the Middle Pleistocene (>500 ka) until at least the MIS 4 (76–59 ka) deposits of Lida Ajer. Thus, while our data do not refute any of the abovementioned hypotheses, this long persistence through major climatic and geological events does suggest that other causes may need to be invoked to explain the extinction of the leopard on Sumatra.

*Tapirus* specimens from the two sites provided reliable minimum ages, meaning that the likely youngest specimen from Djambu is one of the youngest fossils reported from the Padang Highlands caves. *Tapirus* (the tapir) is a medium-sized ungulate that is recovered relatively commonly from the Padang Highlands, and these newly dated records of it, in conjunction with previously dated deposits in that region (Lida Ajer, Ngalau Gupin), indicate persistence of this taxon throughout at least the Late Pleistocene and very probably the Middle Pleistocene.

The *Elephas maximus* records indicate that the Asian elephant has been present in Sumatra since the Middle Pleistocene. Like the tapir, it is a relatively common large mammal recovered from the Padang Highlands caves and is still extant on Sumatra today.

At a site level, the dating resolution of all teeth examined herein is limited—by available techniques and destructive analytical ability; see Duval et al. (2021) for a detailed discussion of dating limitations in these cave environments—such that the geochronological picture that emerges for these sites can be interpreted in several ways. The Sibrambang material produced dates of approximately >52–56 ka, >85 ka, >148 ka, and >165 ka. The Djambu material produced dates of >38 ka, >85 ka, and >500 ka.

The dates obtained from both Sibrambang and Djambu demonstrate a potentially huge chronological range for each site, and it is possible that the teeth from the two sites were each derived from a single massively time-averaged original deposit in each cave (or a single deposit facilitating heterogeneous and complex uranium-uptake histories across incorporated teeth, with Sibrambang >165 ka and Djambu >500 ka). However, we consider it more likely that they came from different deposits in the respective cave systems. Older fossils may have become incorporated into younger assemblages through dissolution and re-formation of breccias in the system (see Louys et al. 2017 and O'Connor et al. 2017 for detailed discussions), such that what may have appeared to be a single deposit was



the amalgamation of two or more palaeodeposits in a single setting. Unfortunately, without detailed field notes of the excavations or re-examination of the caves, determining which of these scenarios is most likely is currently impossible.

In a best-case scenario for the uranium-uptake histories of the teeth, it is most likely that the fossils from Djambu were derived from at least three periods: (1) >500 ka (beyond or close to the limit of the U–Th technique); (2) close to 85 ka (but not younger); and (3) close to 38 ka (but not younger). These could represent different collecting areas in the cave, or one or two massively time-averaged deposits. Sibrambang has a mix of fossils with different ages, and it is hard to determine how many distinct time intervals are present. Conservatively, there are at least two: one >149 ka and a younger one >55 ka (but no younger than that). Unlike the teeth from Djambu, the Sibrambang teeth included none that returned ages that appear potentially close to the true age of the individual.

Despite the huge age ranges demonstrated by the U-series dating, the carbon and oxygen isotope values showed remarkable consistency. Other than a single elephant, all taxa sampled from the sites are indicative of wet, tropical rainforests (as shown by Figure 5.2), quite unlike what would be expected from a Southeast Asian mixed to open woodland site—for example, Tham Wiman Nakin (Louys and Meijaard 2010; Louys and Roberts 2020; Pushkina et al. 2010). This suggests a high degree of stability in the Padang Highlands throughout glacial–interglacial cycles, or that the primary accumulating agent of fossils (likely to be porcupines in all the sites, based on the preservation of almost nothing but tooth crowns; Smith et al. 2020), operated only in rainforest conditions. Previous carbon and oxygen isotope analyses of suid remains from Sibrambang and bovid and cervid remains from unnamed Padang Highlands caves also demonstrated a C<sub>3</sub>-dominated diet for these taxa, although the ingestion of some C<sub>4</sub> vegetation is indicated in at least some of the samples (Janssen et al. 2016). This accords with palaeocommunity analyses of Lida Ajer, Sibrambang, and Djambu that suggest the presence of more open areas in Sumatra during the Pleistocene (Spehar et al. 2018). Importantly, the one elephant sample from Djambu that plotted on the C<sub>4</sub> end of the spectrum (1030i, D004) is also one of two specimens dating to the Middle Pleistocene (i.e. >500 ka). This raises the intriguing possibility that the extensive savanna environments recorded for Southeast Asia during the Middle Pleistocene (Louys and Roberts 2020) may have extended into the Padang Highlands. More fossil deposits of this age will be required to confirm that; however, it hints that there may have been some faunal turnover events in Sumatra similar to those experienced in Java; the record of *Hexaprotodon* at Ngalau Gupin (Smith et al. 2021) supports this hypothesis. Relatively open savanna environments would have provided suitable habitats for several large mammals, including early hominins (Louys and Roberts 2020).

Our results have implications for previous palaeoecological arguments that have been based on these sites. Several researchers, including one present author, have treated each of the Sibrambang and Djambu assemblages as representing a single palaeocommunity for the purposes of palaeoecological analyses (e.g. Bacon et al. 2015; Louys 2012; Volmer et al. 2017). On one hand, the results presented here do not invalidate this treatment—at each site, there is an assemblage of fauna that were found together over a finite period, even if that period cannot yet be precisely bracketed. On the other hand, the large period represented by each site may necessitate critical re-examination of the ecological inferences derived from the deposits. At best, as a single palaeocommunity, Djambu represents a time-averaged assemblage dating from between 38 and >500 ka. At Sibrambang, the time averaging is somewhat better constrained, perhaps to between 55 and >149 ka, but this is probably still too broad to provide convincing evidence for ecological interactions between individuals.

The broad temporal span represented by the assemblages also has implications for the taxonomy of species erected based on fossil material from the caves. In Sumatra, two fossil orangutan species have been proposed from these sites: *Pongo palaeosumatrensis* and *P. duboisi*. The first of these was originally erected by Hooijer (1948) as a subspecies of *P. pygmaeus* (under which all extant orangutans were classified at the time). Hooijer erected this subspecies based on the larger-than-average teeth of the fossil taxon compared to the modern orangutan. In this subspecies, he grouped all the Sumatran samples together and selected as the holotype a left third upper molar ( $M_3$ ) from Simbrambang. Badoux (1959) and Kahlke (1972) argued that the differences between *P. p. palaeosumatrensis* and modern orangutans were insufficient to merit taxonomic distinction. Drawhorn (1995), in his re-examination of fossil orangutans, also noted that the dimensions of orangutan teeth from this site were not significantly different from modern orangutan dental dimensions under a heteroscedastic  $t$ -test. However, Drawhorn (1995) was more circumspect than Badoux (1959) and Kahlke (1972) in rejecting this taxon, choosing to restrict the subspecies to specimens from Sibrambang while raising the possibility that the Sibrambang orangutans may be accommodated by the modern Sumatran orangutan species *P. abelii*. Conversely, Harrison et al. (2014) raised *P. p. palaeosumatrensis* to full species level, largely based on arguments by Harrison (2000), who, like Hooijer, grouped all Sumatran fossil orangutans together in his statistical analysis.

*Pongo duboisi* was proposed by Drawhorn (1995) to accommodate the orangutan fossils from Lida Ajer, which, unlike the Sibrambang sample, were statistically different from modern populations. To this hypodigm, Drawhorn (1995) added the material from Djambu under a subspecies, *P. duboisi djamboensis* (separate from the Lida Ajer subspecies *P. d. lidaajerensis*). Drawhorn also presciently suggested that the Djambu orangutans were derived from two separate assemblages; our results suggest that Djambu may in fact be derived from at least three different periods.

Our results also suggest that the fossil material derived from Sibrambang comes from at least two periods, one of which (at c. 55 ka) may have overlapped with both Lida Ajer and some Djambu fossils (the other, at >148 ka, may have overlapped with other Djambu fossils as well). Because it is not possible to determine which fossil orangutans from Sibrambang belong to which period without resorting to directly dating every specimen, any given orangutan sample from Sibrambang may represent one, two or even more biological populations. The relationship of these populations to orangutans preserved in Lida Ajer and Djambu is unclear, and while it is unlikely that several different species of sympatric ape coexisted in such a small region, we note that less than 100 km currently separates the two extant Sumatran orangutan species (Meijaard et al. 2021). *P. palaeosumatrensis* is only nominally distinguished from other orangutans based on average size (and only from *P. duboisi* if restricting the hypodigm to material from Sibrambang), necessitating a biological population to draw the average from; therefore, since no clear and single population is preserved, we suggest this taxon be considered a *nomen dubium*.

In contrast, *Pongo duboisi* is derived from a stratigraphically and chronologically well-constrained fossil deposit and is therefore statistically differentiable from other orangutans. However, there is an issue regarding the availability of the name *P. duboisi*, which has been described only in an unpublished PhD thesis (Drawhorn 1995). Under International Code of Zoological Nomenclature Article 8.1, for a work to be considered published, it must be issued for the purpose of providing a public and permanent scientific record (8.1.1) and it must have been produced in an edition providing simultaneously obtainable copies by a method that assures numerous identical, durable copies (8.1.3.1). As an unpublished PhD thesis does not fulfil these criteria, until the name is made available, we will refer to the Lida Ajer orangutans as *Pongo 'duboisi'*. Moreover, while *P. 'duboisi' lidaajerensis* derives from a temporally constrained deposit, *P. 'd.' djamboensis* almost certainly does

not. Distinguishing which of the orangutans from Djambu belongs to the *P. 'duboisii'* hypodigm will require more-constrained deposits from Djambu. Thus, like *P. palaeosumatrensis*, this subspecies, even when available, should be considered a *nomen dubium*.

## Conclusions

The Sumatran fossils recovered by Dubois have, until recently, provided the only insights into the island's palaeontological past. They have been interpreted as characteristically rainforest, closed-forest, or humid-forest faunas (de Vos 1983; Louys and Meijaard 2010), similar if not identical to those found today on the island. Despite a lack of detail about the age or geological context of the fossil assemblages from Sibrambang, Djambu and, until recently, Lida Ajer, these assemblages have continued to be used to infer environmental and ecological processes occurring in Pleistocene Southeast Asia. Our stable isotope results indicate that the Dubois fossil materials from Sibrambang and Djambu largely represent characteristically rainforest species and that such conditions have been present on the island since the Middle Pleistocene. The only exception is an elephant fossil hinting at more open conditions. Our dating results from these sites are less clear-cut. Nevertheless, they suggest that fossils were deposited during several periods in both caves, from at least the Middle Pleistocene until the Late Pleistocene. Moreover, they indicate that relatively open environments may have been present in the Padang Highlands during the Middle Pleistocene. These results are important for understanding the ecological and biological history of large mammals on this island and, by implication, of the hominins that would have been present in the broader region.

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