

Early Hominin Biogeography in Island Southeast Asia

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Island Southeast Asia covers Eurasia's tropical expanse of continental shelf and active subduction zones. Cutting between island landmasses, Wallace's Line separates Sunda and the Eastern Island Arc (the Arc) into distinct tectonic and faunal provinces. West of the line, on Sunda, Java Island yields many fossils of *Homo erectus*. East of the line, on the Arc, Flores Island provides one skeleton and isolated remains of *Homo floresiensis*. Luzon Island in the Philippines has another fossil hominin. Sulawesi preserves early hominin archeology. This insular divergence sets up a unique regional context for early hominin dispersal, isolation, and extinction. The evidence is reviewed across three Pleistocene climate periods. Patterns are discussed in relation to the pulse of global sea-level shifts, as well as regional geo-tectonics, catastrophes, stegodon dispersal, and paleogenomics. Several patterns imply evolutionary processes typical of oceanic islands. Early hominins apparently responded to changing island conditions for a million-and-a-half years, likely becoming extinct during the period in which *Homo sapiens* colonized the region.

In 1859, Alfred Russell Wallace identified two faunal provinces within Island Southeast Asia (ISEA),

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Sunda and the Arc. Wallace's Line represents a series of sea-channel barriers to the dispersal of large mammals between them. The provinces are based primarily on the continental origin of large terrestrial mammals (Fig. 1, Box 1).¹ West of Wallace's Line, mammalian species have Eurasian origins; east of the line, "Wallacean" mammals and other vertebrates show a mixture of Eurasian and Australian origins. Similar, if less provincial differentiation can be observed for some species of fish, insects, and birds. The line should pose a factor for ISEA early hominin dispersal, isolation, and extinction.

EARLY HOMININ BIOGEOGRAPHY IN ISLAND SOUTHEAST ASIA

In 1891, Eugene Dubois' named *Pithecanthropus erectus* (now *Homo erectus*) based on a calotte and femur found at Trinil, in the Solo Basin of eastern Java.² Sangiran, also in the

Solo Basin, has since produced more than 80 *Homo erectus* cranial and dental fossils. The Sangiran and Trinil fossils have thick cranial vaults and cranial capacities of 840 to 1,059 cc.³ A much later set of Solo Basin *Homo erectus* fossils, from Ngandong and related sites, have cranial capacities reaching 1,250 cc.

In 2003, at Liang Bua, on Flores, east of Wallace's Line, *Homo floresiensis* was defined on the basis of one nearly complete skeleton and fragmentary remains of several individuals.^{4,5} Compared to Sunda *Homo erectus*, the fossils from Liang Bua have a very small cranial capacity (417 cm³). In relation to most Pleistocene early hominins, the Liang Bua skeleton is short (1.06 m) and has primitive wrists and large feet, as well as a late age (~60 ka).⁶ Other members of the Liang Bua vertebrate fauna share similar insular characters (Box 2).⁶ When compared with related species on other ISEA landmasses, the Liang Bua fauna show signs of isolation on Flores for a significant part of the Pleistocene.⁷

In 2007, fragmentary fossils were collected from Callao Cave on the island of Luzon, in the Philippines.⁸ Because of its small dimensions and gracile morphology, a complete metatarsal resembles those in small-bodied early hominins, including *Homo habilis* and *Homo floresiensis*. Its date, 66.7 ka, is close to that of Liang Bua. In 2014, an upper molar tooth row of archaic character was recovered, as were additional small limb bones.⁹ The new Callao finds suggest a possible third group to the ISEA Pleistocene hominin population

Key words: Sunda; insular dwarfism; island rule; *Homo erectus*; *Homo floresiensis*; Marine Isotope Stages (MIS); Java; Flores; Luzon; Sulawesi; Timor

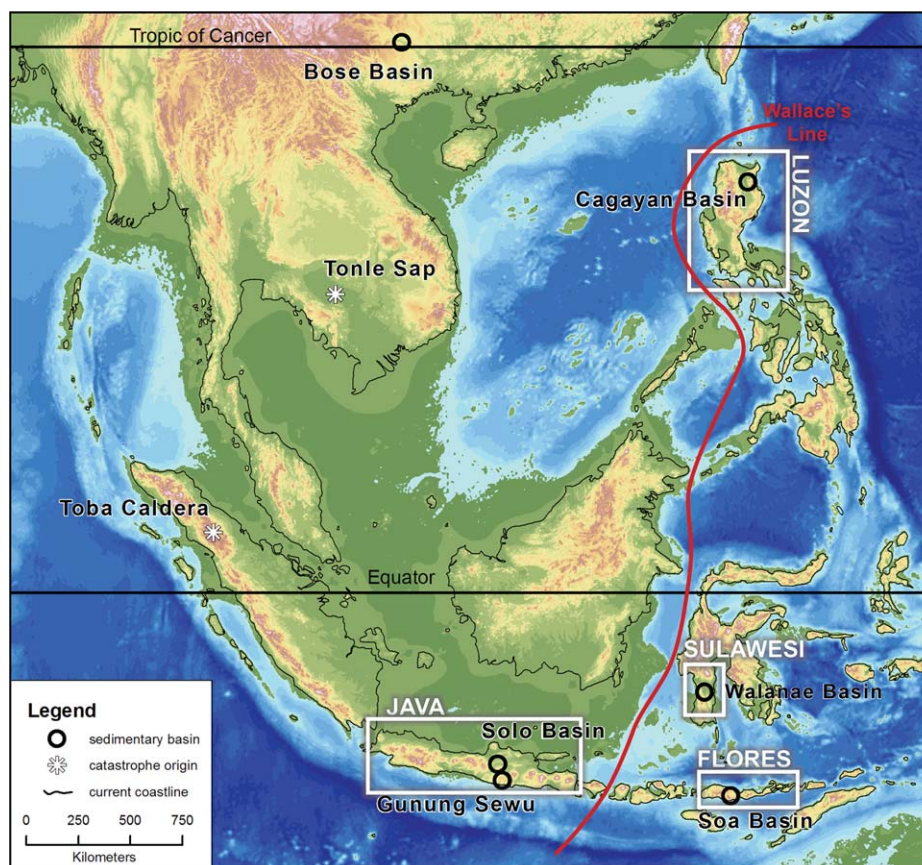


Figure 1. Southeast Asia: sedimentary basins and catastrophe origin points of relevance to early hominin paleoanthropology. Terrestrial surface extends to 100 m below current sea level. We followed Huxley's modification of Wallace's Line²⁰⁸ as illustrated in Cooper and Stringer²⁰⁴. Boxes show areas detailed in Figure 3. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

and a second colonization east of Wallace's Line.

Early hominins are now definitively situated on Sunda and at two widespread points on the Arc. Both Arc fossil hominins have the small size and specialized skeletal traits seen in insular evolutionary contexts and, to a lesser extent, in the earliest *Homo erectus* from Eurasia (Dmanisi). The Arc hominins diverge greatly from all known Sunda forms. After more than a century of accumulating fragmentary evidence, ISEA early hominin biogeography is now a significant research topic. Here we review relevant evidence from Sunda and the Arc within a framework of Pleistocene climate change, our primary goal being to evaluate potential roles for well-known insular evolutionary processes in ISEA early hominin evolution (Box 2).

While ISEA early hominin fossils are few and spatially isolated, Pleistocene-age stone artifacts are

numerous and widespread. Archeology therefore fleshes out early hominin biogeography. The historical trend of archeological research parallels that of fossils. Recent research provides a richer comparative base (Box 3). Stone tools are incorporated into the review when an excavated stratigraphic sequence contains fauna and artifacts within a recognized geological level and when a sequence-long sampling strategy has consistently produced Pleistocene ages.

Using dated Marine Isotope Stages (MIS) global events and a long chronology for regional occurrences, we can begin to comprehend ISEA biogeographic events in their global contexts (Fig. 2, Box 4). Three global events can be tied to crucial regional biogeographic transitions: the Olduvai paleomagnetic event, the Late Early Pleistocene Revolution (aka Mid-Pleistocene Revolution), and the Mid-Brunhes Event. This review has

three sections corresponding to these events. A period framework makes for some repetition in presenting sites with long stratigraphic sequences. Nevertheless, parsing regional developments by period helps to identify the effects of climate change and several regional environmental catastrophes (Box 5). Figure 2 presents the overall scheme. Each period section has a synoptic table for the relevant events, sites, lithics, and fauna. Table 1, for example, presents the earlier Pleistocene benchmarks.

OLDUVAI SUBCHRON, OR EARLIER PLEISTOCENE

During the earlier Pleistocene (~2.6-0.9 Ma), a 41-kyr orbital cycle drove global climate. This periodicity, based on earth's orbital obliquity, exemplifies one of three such orbital patterns, known as Milankovitch cycles.¹⁰ During this time, glacial-

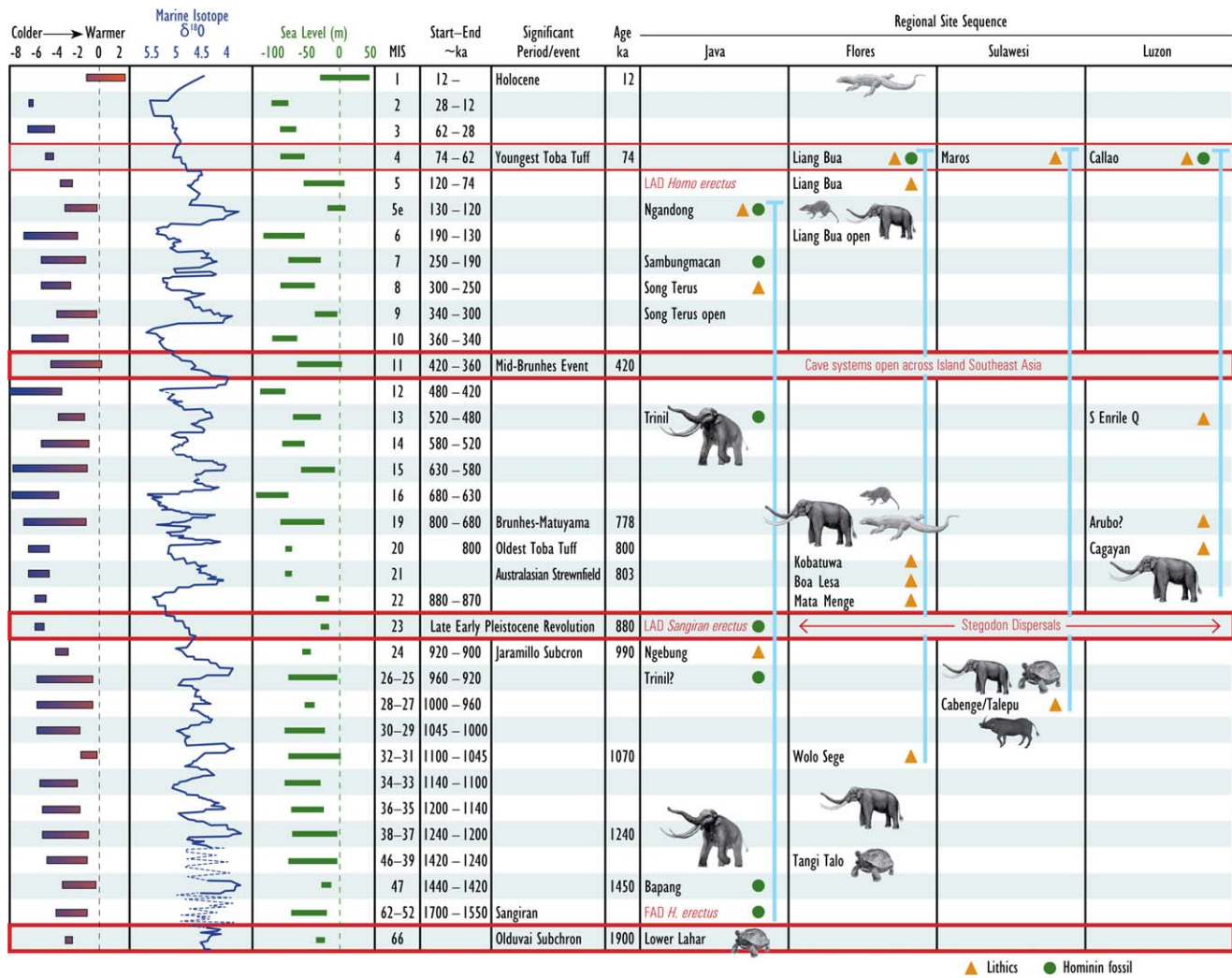


Figure 2. ISEA Pleistocene chronology and site correlation. Even-numbered MIS represent cooler phases (Northern hemispheric glacials); odd-numbered stages represent warmer phases (Northern hemispheric interglacials). MIS ages are drawn from Bowen and Sikes,²⁷² Berger *et al.*,¹⁰⁹ and Willoughby,²⁷³ Ages before MIS 19 are approximate. Since early hominin fossils are known only from sites in Java and Liang Bua, Flores, artifacts serve as the evidence of early hominins at other sites. FAD = first appearance datum; LAD = last appearance datum. Except where noted, site or event placement marks earliest occurrence. Blue lines indicate presumed hominin continuous occupation in each regional site sequence unless otherwise noted. Sites with named formations and/or geologic designations: **Lower Lahar**, Lower Lahar Unit (Sangiran Formation); **Sangiran**, Sangiran Formation; **Bapang**, Bapang Formation; **Ngebung**, Bapang Formation; **Song Terus**, karst cave; **Ngandong**, 20 m terrace of Solo River; **Wolo Sege**, **Tangi Talo**, **Mata Menge**, **Boa Lesa**, and **Kobatuwa**, Ola Kile Formation; **Liang Bua**, karst cave; **S Enrile Q**, Awidon Mesa Formation; **Cagayan**, Ilagan and Awidon Mesa Formations; **Arubo**, Sierra Madre foothills; **Callao**, karst cave; **Cabenge**, Wanae Basin fill. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

interglacial cycles were relatively short and had low temperature amplitude.^{11,12} Toward the middle of this phase, the Olduvai Subchron marks a brief geomagnetic pole reversal event, 1.98-1.79 Ma.¹³ Soon after Olduvai, increases in monsoon intensity were recorded in the terrestrial contexts of the Lake Turkana (Kenya) and Heqin (China) basins.^{14,15} Glacial-interglacial cycling had an increased effect on

the size and distribution of Sunda landmasses. Northern Hemisphere glacial ice advanced significantly between about 1.8 and 1.74 Ma (MIS 62, 60, and 58), about 1.56 Ma (MIS 52), between 1.24 and 1.1 Ma (MIS 36, 34, and 30), and about 0.9 Ma (MIS 22).¹⁶ During these stages, sea-level lowstands opened emergent landmasses throughout ISEA.^{17,18} It was, apparently, just after the Olduvai event that Pleistocene Eurasian

mammals arrived on an emergent Sunda.¹⁹⁻²¹

Sunda

Sangiran, Java (Indonesia)

Much of the Solo Basin lies at about 7° S latitude and sits above the Indonesian subduction zone (Fig. 3A). Mammalian fossils are preserved within a 500,000-year

Box 1. Geomorphologic Setting

ISEA encompasses Sunda and the Arc. ISEA is the result of the Indian and Pacific oceanic plates subducting under the Eurasian terrestrial plate. Regional topography ranges from broad coastal plain and continental shelf to volcanic islands, plateaus, and deep sea trenches (Figs. 1 and 8).

Sunda: Much of the Indonesian Archipelago lies on the Sunda shelf, a vast, now mostly submerged southward extension of the Eurasian continental plate.^{206,207} The continental shelf extends southward from the present Southeast Asia mainland toward Java and the Indian Ocean (8.1° S). Here, the term “Sunda shelf” is reserved for the continental projection, while “Sunda” refers to the shelf’s island landmasses. The term “Sunda” updates the nineteenth-century names of “Sundaland” and “Sunda Land.” Today, Sunda takes in the current large landmasses of the Malay Peninsula, Borneo, Sumatra, and Java, as well as smaller islands such as Bali.

Eastern Island Arc: East of Sunda, the sea bottom is complex with trenches and ranges. The landmasses of this area constitute the Arc, which stretches from

Luzon in the north, southward through Sulawesi and the Maluku Islands and, in the extreme south, to Flores, Sumba, Timor, and related small islands. Much of the Arc lies in Wallacea, the geographic and ecological transition zone between Sunda and Sahul (Australia and New Guinea).²⁰⁸ During the Pliocene and Pleistocene, especially during periods of glacio-eustatic sea-level drawdown, large mammals, including primates, evidently penetrated current marine barriers between Sunda and Wallacea.^{209,210} Fossil and archeological evidence indicates that early hominins traversed current straits numerous times during the Pleistocene.

Eustasy, Tectonics, Volcanism: Glacio-eustatic sea level changes of ~125 m are documented for the Pleistocene.²¹¹ Glacial eustasy repeatedly redistributed habitable island landmasses and interisland connections. Glacial period sea-level lowstands maximized conditions for regional dispersals. Interglacial highstands separated early hominin groups and set up conditions for insular endemism. Several subduction zones have made for deep sea barriers of full Pleistocene duration. Trending north-south to

create Wallace’s line are the Mindoro Strait, Sulu and Celebes Seas, and the Makassar and Lombok Straits. Trending east-west are the Flores and Banda Seas and, south of Flores, the Savu Sea.

Regional tectonic events may have been involved with specific and short-lived dispersal pathways. Sartono implicated small-scale uplift in relation to dispersal corridors along the Palawan, Sulu, Sangihe, and Selayar archipelagos (Fig. 8).⁸⁵ While this particular model is now dated, small-scale tectonic effects could be approached in new terms. Within the area covering the Seas of Java, Banda, and Molucca (Fig. 8), there are numerous platelets with active convergent and divergent boundaries.²¹² Such platelets are subject to forming pop-up blocks.²¹³ This process could have enhanced the formation of lowstand land bridges. Regional tephra catastrophes could rearrange local habitats. The Sunda sedimentary record shows frequent volcanic eruptions along plate margins after the Olduvai Subchron. Truly large emissions could extend local landmasses seaward, providing larger lowland areas and, in some cases, small land bridges.²¹⁴

sequence (~1.53-0.98 Ma) of aggrading volcanoclastic sediments.¹⁹ Currently, more than 80 fossil fragments of *Homo erectus* are known from Sangiran (Fig. 4). The area has three primary sedimentary deposits: the Lower Lahar Unit, the Sangiran Formation, and the Bapang Formation.

Lower Lahar Unit. As early as 1.90 Ma, a nearby volcanic cone, produced a massive lahar-type debris flow. Sangiran represents a relatively distal point of the flow, where the lahar entered marine conditions on Sunda’s south coast. Incorporated fossils indicate that the lahar pushed through numerous environments before arriving at Sangiran. A cervid

mandibular fragment reflects terrestrial conditions in the higher reaches.²⁰ Freshwater mollusks indicate swamps or shallow lakes in the lower reaches.²² Sangiran itself reflects near-shore marine environments transformed into estuarine and marsh settings. Shortly thereafter, glacio-eustatic sea level regressions exposed lahar-infilled lagoons and near-shore environments to create terrestrial habitats.²³ Since neither hominin fossils nor stone artifacts were incorporated, it is assumed that the Lower Lahar Unit predates the arrival of *Homo erectus*.

Sangiran Formation. A sequence of dark-colored lacustrine siltstones,

and thin tuffs overlies the Lower Lahar Unit. These represent slow-moving streams draining nearby low volcanic highlands into shallow lakes. Such watercourses intermittently flooded lake margins and marshes, transforming coastal lagoons into inland lakes. Occasional volcanic eruptions deposited thin blankets of ash. Lake-edge and marsh environments supported sedges, ferns, water-tolerant grasses, and trees.^{24,25} The associated fauna comprised aquatic and semi-aquatic vertebrates such as pygmy hippo (*Hexaprotodon*), crocodile (*Crocodylus*), and tortoise (*Geochelone*), as well as turtle and fish (fragmentary remains).^{21,26-28} Wet grasslands with scattered shrubs

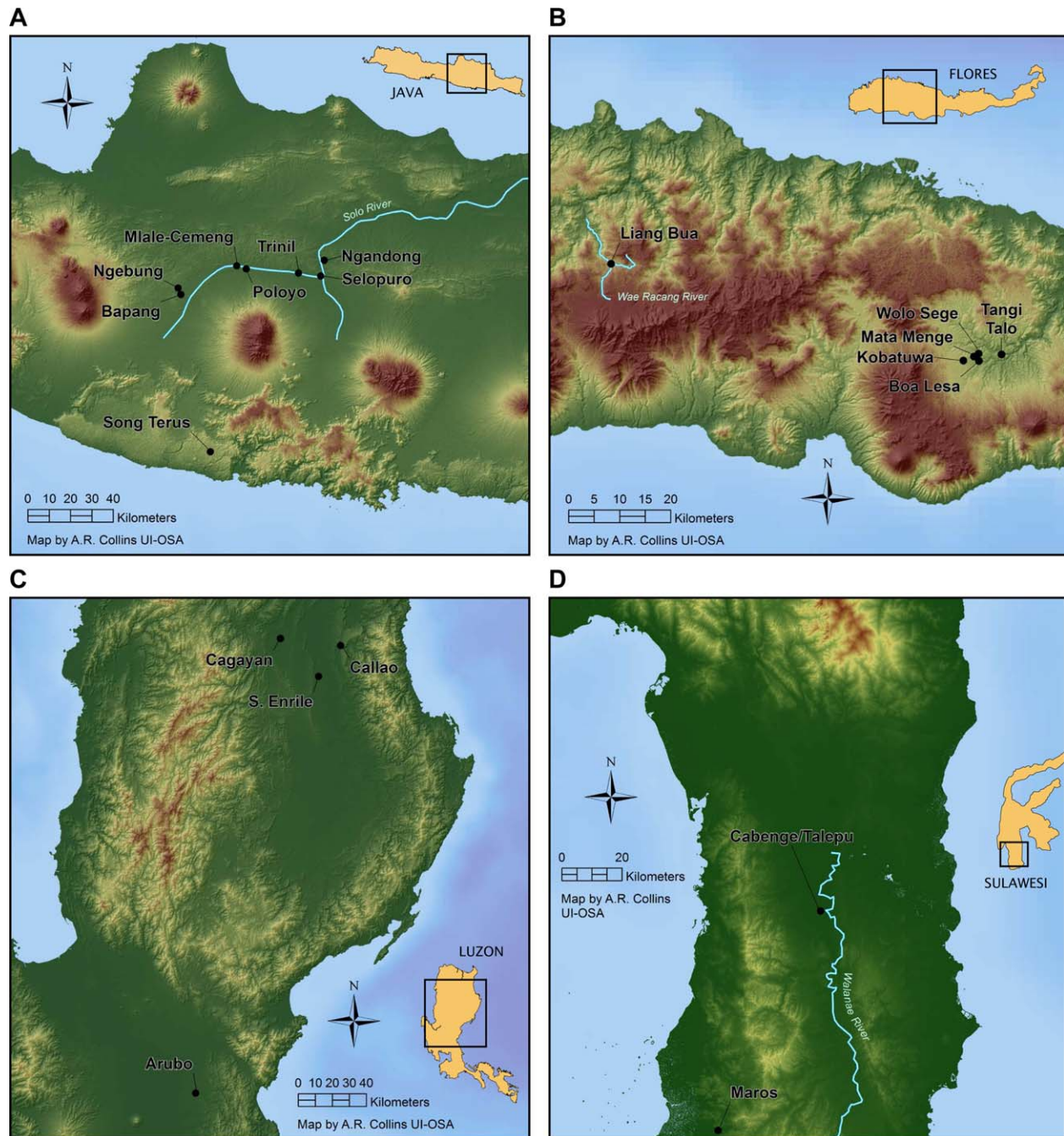


Figure 3. ISEA early hominin sites: A, central/eastern Java; B, central Flores; C, northern Luzon; D, southwest Sulawesi. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

occupied slightly higher landscapes. Still higher, better-drained parts of the landscape supported a community of sedges, grasses, ferns, and scattered trees.²⁹ Fauna included stegodon (*Stegodon elephantoides*), cervids (*Cervus zwanni*, *C. hippelaphus*, and *Cervus* sp. indet.) and one small bovid (*Duboisia santeng*), as well as *Homo erectus*.^{19,26,27,30} The hominin-bearing

upper reaches of the formation date to between 1.66 and 1.57 Ma.²³

At Bukuran, apparent technological cutmarks have been observed on bovid bones from legacy collections. Two specimens show marks outside the range of natural causes. While stone tools are absent from the Sangiran Formation, molluscan shells are abundant. In a series of experi-

ments, clamshell cutting tools best replicated the Bukuran bovid bone cut marks.³¹

Bapang Formation. Between 1.6 and 1.5 Ma, volcanic cones grew north-west and southeast of Sangiran. Larger, more powerful streams began scouring and infilling the local lowlands.²³ A stark fluvial erosion



Figure 4. *Homo erectus* cranium (S 17): Bapang Formation below the Middle Tuff, Sangiran, Solo Basin, Java. Cranial capacity: 1,004 cc.²⁷⁴ (Photograph: R. Ciochon). (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

surface often marks the contact between the Sangiran and Bapang Formations. This contact represents a period of net sediment removal from the Sangiran area.²⁹ Immediately above the contact, the Grenzbank Zone has poorly sorted coarse sediments. Heavy clasts, including vertebrate fossils, can be highly fragmented and indicate multiple reworking. Hominin fossils are found throughout the Bapang. However, in comparison with higher reaches of the formation, the Grenzbank lacks hominin skeletal elements of relatively low density, such as calottes, and retains only the denser mandibular and maxillary fragments and teeth. ⁴⁰Ar/³⁹Ar radiometric analysis suggests that the deposit began accumulating more than 1.5 Ma and continued to 0.9 Ma,¹⁹ thus recording climate cycles in the range of MIS 47–23.

The Bapang sequence contains numerous paleosols. These developed on riverine landscapes, representing riparian forest, savanna, and open woodland environments.²⁹ Paleosol morphology and carbon isotope values indicate a long-term shift toward longer annual dry seasons.²⁹ The more open habitat supported carnivores (*Panthera*), pigs (*Sus brachygnathus*), cervids (*Axis lydekkeri*),

large bovids (*Bubalus palaeokerabau*, *Bibos palaesondaicus*), stegodon (*Stegodon trigonocephalus*), and primates (*Homo erectus*, *Macaca* sp. indet., *Trachypithecus* cf. *auratus*).^{27,32,33} After about 0.9 Ma, Pohjajar Formation fluvial deposits covered the Bapang sequence with a higher proportion of air-fall tuffs, fluvially reworked ash fall, and lahar deposits (Fig. 2). The Pohjajar has not yielded *Homo erectus* remains at Sangiran or elsewhere.

Trinil, Java

In its middle course, the Solo River makes an abrupt northward turn to cut through the Kendeng Hills (Fig. 3A). In 1891, Eugene Dubois made the Java Man discovery of a calotte and femur on the Solo River bank at Trinil. Dubois named the collection deposit the *Hauptknochenschicht* (main bone layer) of Trinil.^{34,35} Much later, four more femora were collected in the same area.^{36–38} The Trinil skullcap lies within the range of morphological variation for the large collection of Sangiran specimens. Together, the Sangiran and Trinil crania should represent the earlier Sunda *Homo erectus* paleodeme.

The stratigraphic relationship among the fossils has always been questioned, especially between the calotte and the original Femur I.^{39,40} Recently, all five Trinil femora have been morphologically compared and their structural and density characteristics evaluated by computed tomography.⁴¹ Femur I is anatomically more modern and less fossilized than Femora II–V. Femur I is apparently younger than the calotte, while Femora II–V may be more closely related in time to the *Homo erectus* calotte.⁴¹

Trinil has seen little field investigation since 1891. The stratigraphy remains unimproved and contention persists about the age of *Hauptknochenschicht*. The main bone layer is now considered an overbank deposit built up during repeated floods. It may contain materials of different origins and ages.^{42,43} The Dubois fauna collection, curated at the Reiks Museum in Leiden, has been inten-

sively studied. Old endemic species include *Duboisia santeng* and *Axis lydekkeri*, as well as *Stegodon trigonocephalus*, *Bubalus palaeokerabau*, *Bibos palaesondaicus*, *Sus brachygnathus*, and *Panthera tigris trinilensis*.^{26,44} The assemblage has been compared with that of the Bapang formation Grenzbank Zone, having an age, using the short chronology, of around 1.0 Ma.²⁶ The long chronology places the Grenzbank Zone at 1.5 Ma (Box 4).¹⁹ In any event, comparison with the Sangiran sequence is of limited value.

Using Trinil and other legacy faunal collections, Storm modeled the ecological role of ISEA *Homo erectus*.⁴⁵ The number of identified specimens and the minimum number of individuals reflect trophic levels of primary and secondary consumers. Further, the numbers of remains of *Homo erectus*, at sites such as Sangiran, resemble those of large carnivores. These numbers suggest that *Homo erectus* functioned as a carnivorous omnivore.⁴⁵

A recent analysis of curated *Hauptknochenschicht* materials is provocative. Results suggest a significantly younger age for the site and that *Homo erectus* made complex use of freshwater shellfish. ⁴⁰Ar/³⁹Ar and luminescence dating methods have been applied to sediment adhering to freshwater mollusk shells (*Pseudodon*) in the surviving faunal collection.⁴⁶ The results are indicative of the Mid-Brunhes Event (~480 ka). As the new age analysis depends on materials removed from stratigraphic context, it is difficult to make a definitive judgment. The dates and behavioral hypothesis are presented in the Mid-Brunhes Event section.

Eastern Island Arc

Soa Basin, Flores (Indonesia)

The Soa Basin covers 200 km² of west-central Flores and contains two volcanoclastic sedimentary units. At its base, the Ola Kile Formation consists of andesitic breccias and volcanic mudflows with minor interbedded tuffaceous siltstones, sandstones, and lava flows.⁴⁷ From near the top of the formation,

Box 2. Insular Evolutionary Process

Oceanic islands are isolated settings in which natural selection and genetic drift can intensify and thus accelerate evolutionary rates. Immigrating island populations are smaller and less genetically diverse than the mainland source population, resulting in a founder effect. Islands have lower biodiversity than do mainland areas, which results in species expanding and shifting ecological niches from their mainland counterparts. Moreover, island size is linked with faunal turnover, with smaller islands having higher extinction rates.²¹⁵ These conditions force microevolutionary changes that may lead to macroevolutionary changes, including speciation. Van Valen's "island rule" observes that in long-term island contexts, large-bodied mammals tend to become smaller and smaller ones bigger.²¹⁶ The effects of the island rule tend to be inversely proportional to an island's

size²¹⁷ and positively correlated with its degree of isolation from the mainland.²¹⁸ The smaller and more isolated an island, the more significant the role of island rule.

Island dwarfing has been observed in a wide variety of both living and fossil mammals. There are well-known cases of Pleistocene proboscidean dwarfing relating to Pleistocene sea-level fluctuations. These include elephants on several Mediterranean islands, mammoths on the California Channel Islands, and stegodons in Island Southeast Asia.

The strong hypothesis for island dwarfing revolves around population size versus food availability.²¹⁹ In general, island landmasses offer relatively reduced nutritional resources to relatively small populations. Islands also tend to have fewer large predators. In general response, mammals have fewer young, while patterns of body size evolution are much accelerated.²²⁰

This is because large-bodied individuals use more resources, so island natural selection favors smaller individuals which, over time, produce smaller-bodied populations.²²¹ Smaller body size aids in maintaining relatively large populations on island resource bases.²²²

Pleistocene ISEA demonstrates numerous cases of island endemism. At least five dwarfed species of *Stegodon* emerged in the region. Van Valen's island rule is directly applicable in the large and small forms observed in the Liang Bua vertebrate fauna.^{6,216} These include giant tortoise (*Geochelone*), giant rat (*Spelaomys* or *Hooijeromys nusatenggara*), a very small stegodon (*Stegodon florensis insularis*), and the dwarfed hominin *Homo floresiensis* (Box 6). As a dwarf hominin, Liang Bua *Homo floresiensis* fits well within its ISEA ecological and evolutionary context.⁶

a fission-track analysis provides a minimum age of 1.86 ± 0.12 Ma. Above Ola Kile, the Ola Bula Formation comprises 100 m of volcanic and fluvio-lacustrine deposits. Like the Solo Basin Bapang Formation, the Ola Bula is highly volcanoclastic and indicates young riverine habitats and the presence of lakes. Two Soa Basin sites, one archeological and one paleontological, reveal Flores sedimentary and faunal environments toward the end of the Early Pleistocene (Fig. 3B).

Tangi Talo. This paleontological locale lies low in the Ola Bula stratigraphic sequence. Fauna include dwarf *Stegodon* (*Stegodon sondaari*), giant tortoise (*Geochelone*), and Komodo dragon (*Varanus komodoensis*). There are no signs of butchering and no stone artifacts. The Tangi Talo small-bodied *S. sondaari* is the earliest stegodon on Flores. An overlying tuff of volcanic debris is dated

to 0.90 ± 0.07 Ma.⁴⁸ Dating analyses continue at Tangi Talo, with new results based on ⁴⁰Ar/³⁹Ar eruption age suggesting 1.3 Ma.⁴⁹

Wolo Sege. This archeological site lies in the Ola Bula basal tuff interval, just above the Ola Kile breccias. The sedimentary environment is highly volcanoclastic and represents a stage before the fluvial-lacustrine landscapes had truly developed. Wolo Sege has *in-situ* stone artifacts, including some Acheulean-like implements⁵⁰ (Fig. 5). There is no *in-situ* fauna. Overlying the artifact layers is an ignimbrite with an ⁴⁰Ar/³⁹Ar eruption date of 1.02 ± 0.02 Ma.⁴⁷

The Soa Basin's Ola Bula deposits provide the oldest record of Pleistocene fauna and stone tools east of Sunda. The Wolo Sege artifacts indicate that hominins arrived on Flores well before 1.0 Ma. The young volcanic environment represents the conditions that hominins and other

large mammals encountered on entering Flores.⁴⁷

Walanae Basin, South Sulawesi (Indonesia)

Cabenge. The Walanae Basin lies on Sulawesi's southwest peninsula (Fig. 3D). In the late 1940s, H. R. van Heekeren collected surface stone artifacts and fauna near the village of Cabenge (formerly Tjabenge). The Walanae fauna included giant tortoise (*Testudo morgae*), pygmy elephant (*Archidiskodon celebensis*), stegodon (*Stegodon sompoensis*), giant pig (*Celebochoerus heekereni*), and dwarf buffalo (*Anoa depressicornis*).⁵¹ Although the presence of *Archidiskodon* suggested an earlier Pleistocene age, Van Heekeren linked the Tjabenge stone tool industry with this fauna.⁵² He cautioned, nevertheless, that the Walanae *Archidiskodon* could represent a Middle Pleistocene descendant of a long-

TABLE 1. Early Pleistocene Synoptic Chart

MIS	start ~ka	end ~ka	events	age ka	Java			Flores			Sulawesi			
					sites	lithics	Stegodon	sites	lithics	Stegodon	sites	lithics	Stegodon	trends
24	975	920	EPR / Jaramillo	990				Soa eruptions				Cabenge	small flake (Tjabenge)	<i>S. sompoensis</i> larger N hemisphere ice volumes
31	1070				Trinil		<i>S. trigonocephalus</i>	Wolo Sege	radial cores					significant glaciation/ draw-down
36	1200													significant glaciation/ draw-down
37	1240													
46-38	1400	1250						Tangi Talo					<i>sondaari</i>	
47	1450		Sangiran eruptions		Bapang	small flake (Sangiran)	<i>S. trigonocephalus</i>							
62-52	1700	1550			Sangiran		<i>S. elephantooides</i>							significant glaciation/ draw-down
66	1980	1790	Olduvai subchron		Lower Lahar			Ola Kile fm						Dmanisi <i>H. erectus</i> begin 41-kyr obliquity cycle: glacial cycles of short duration and low temperature amplitude

lived endemic island form. Questions arose about the association of the industry with the fauna and the age of each.⁵³⁻⁵⁶ With new research, the Walanae terraces are now interpreted as the upper part of a normal basin fill sequence uplifted during the Late Pleistocene.³² New work at nearby Talepu suggests that some artifact horizons have an early Pleistocene age.⁵⁷

The Walanae basin volcanoclastic gravel series displays clasts of yellow chalcedony and red jasper. These and other highly colored, fine-grained siliceous rocks are the raw materials for the Tjabenge Industry.⁵² Tjabenge flakes are relatively small and thick, with signs of having been struck in all directions from irregular cores. Tool types include points, concave scrapers, core and keeled scrapers, endscraper picks, and chopping tools. Van Heekeren noted similarities between the Tjabenge and Sangiran flake industries, including the use of small, highly colored, fine-grain raw materials and the production of irregular cores. He concluded that these and other similar flake industries were produced by a single species of hominin⁵² (Fig. 5).

LATE EARLY PLEISTOCENE REVOLUTION OR LATE EARLY- EARLY MIDDLE PLEISTOCENE

The MIS 24-22 complex (~1.0-0.9 Ma) marks a shift in glacial-interglacial forcing from the 41-kyr obliquity-based cycle to a 100-kyr eccentricity-based cycle.¹⁵ The MIS 24-22 complex has thus been called the late Early Pleistocene Revolution (EPR) or the Mid-Pleistocene Revolution.⁵⁸⁻⁶¹ The full period of transition, 1.25 Ma to 700 ka, has been termed the Mid-Pleistocene Transition.⁶²⁻⁶⁴ We call it the "late Early-early Middle Pleistocene."

After EPR, glacial periods became longer and more evenly distributed. Longer glacials served to increase global ice volume, thereby pushing sea-level lowstands as much as 50 m lower than during the earlier Pleistocene.⁶² Short but warm interglacials decreased ice volume quickly. The

Box 3. Stone and Shell Tool Technology

Pleistocene ISEA stone tool assemblages are of three types.

1. Flake Industries. Early surface collecting at several locations have led to this category, in which flake and cobble tools are generally *ad hoc* in flake production and bifacial reduction. Flake industries have relatively few biface and cleaver-type tools.^{54,55,75} Flake industries show neither chronological development nor regional differentiation.

Of relevance are the flake industries named after their modern settlements of Cabenge (Sulawesi), Kota Tampan (Malay Peninsula), and Ngandong and Pacitan (Java). Questions of artifact age and veracity plagued the early surface finds. Late twentieth-century examinations of terrace structure and assemblage technology generally ascribed these surface finds to the late Pleistocene.^{53–55,75} Recent research, nevertheless, has recovered stone tools in association with fauna and, sometimes, datable material. Generally speaking, the earliest well-dated archeological assemblages on both sides of Wallace's Line have ages greater than 900 ka. This pattern holds for Java,⁶⁶ Flores,⁴⁷ and Sulawesi.⁵³ The earliest stone-tool horizon on Luzon is about 800 ka.^{97,101}

2. Large-Flake Acheulean (LFA). This category is defined by the biface- and cleaver-rich site of

Gesher Benot Ya'aqov (GBY) in Israel.^{73,74} The LFA *chaîne opératoire* arrives at simple yet effective cutting tools in a small number of well-structured steps. LFA assemblages feature large (>10 cm) flakes, either raw or minimally retouched as unifacial tools and simple Acheulean-type bifaces (convergent tip) and cleavers (broad tip). The LFA is associated with coarse-grain quartzite and related materials rather than fine-grain flint. Kombewa flake types are common as cleaver blanks.

As a cultural force, the LFA appeared by 1 Ma at Olorgesailie and spread throughout Africa and beyond. While timing is imprecise, the LFA arrived in the Levant, Iberia, and India by ~600 ka. After 500 ka, only sub-Saharan Africa holds sure LFA sites.^{73,74} Recently, the LFA profile has been applied to assemblages from Ngebung (Sangiran, Java) and Gunung Sewu. The attribution was based on typological grounds and a perceived link between the Pinjor fauna (associated with LFA sites in India) and the "*Stegodon-Homo erectus fauna*" of Sunda.²²³ Bifaces and cleavers from the Cagayan and Arubo basin sites (Luzon) have also been termed Acheulean and even Large-Flake Acheulean.^{103,104} Similar tools from Wolo Sege (Soa Basin, Flores) are also called Acheulean.⁷⁸ The question remains of whether or not Acheulean-like tools and reduction

sequences represent a Far East manifestation of the Acheulean cultural formation.

3. Radial-Core Reduction. This is present on Flores, particularly at Mata Menge and Liang Bua. Lithic resources were brought to the site in the form of flake blanks. The Acheulean-like elements of Wolo Sege are not present at Mata Menge, where the more complex tools show a reduction sequence based on centripetal or radial removals on the blanks.⁴ A radial reduction sequence is found again at Liang Bua, 50 km to the west and ~800 kyr later.

ISEA has few Pleistocene archeological sites in which complex stone-tool technology is associated with diverse occupation debris. Several explanations have been offered. Early hominins maintained a vegetarian diet that did not require complex stone tools.²²⁴ Early hominins used more readily available nonlithic raw material, such as bamboo²²⁵ and wood.²²⁶ Since the late 1990s, evidence has mounted to support the use shellfish for food and shells for tools. Shell archeology has been published for three sites: Bukuran and Trinil on Java, and To'os on Timor.^{31,46,87,227} Individually, each site has marginal evidence of shell use. When pooled, a hypothesis for early hominin shellfish use can nevertheless be entertained.

MIS 23 interglacial is therefore implicated in flooding insular landmasses.⁶⁵ At Heqin (China), 0.92 Ma marks the transition to a long period (0.92 to 0.13 Ma) during which the Indian Summer Monsoon (ISM) was structured by both southern high and northern low pressure. During this period, ISM maxima coincided with Northern Hemisphere ice volume minima (interglacials) and Antarctic temperature maxima.¹⁵ Early Middle Pleistocene glacial sea-level

lowstands likely made for extensive dispersal corridors. Likewise, early Middle Pleistocene interglacial highstands led to insular isolation and endemic evolution.

The early Middle Pleistocene may also be associated with generally lower sedimentation rates. In the basins of Soa (Flores) and Cagayan (Luzon), the period immediately surrounding the EPR is well represented by open-air archeological and faunal sites, but evidence of hominin habi-

tation trails off rapidly thereafter. The EPR marks the last known occurrence of *Homo erectus* at Sangiran. The early Middle Pleistocene saw two region-wide catastrophes: the Australasian tektite impact and the oldest Toba Tuff super-eruption (Box 5).

Two areas, Sangiran and Soa, have sedimentary sequences that extend from the Early to the Middle Pleistocene. Earlier, we presented Early Pleistocene evidence. We now

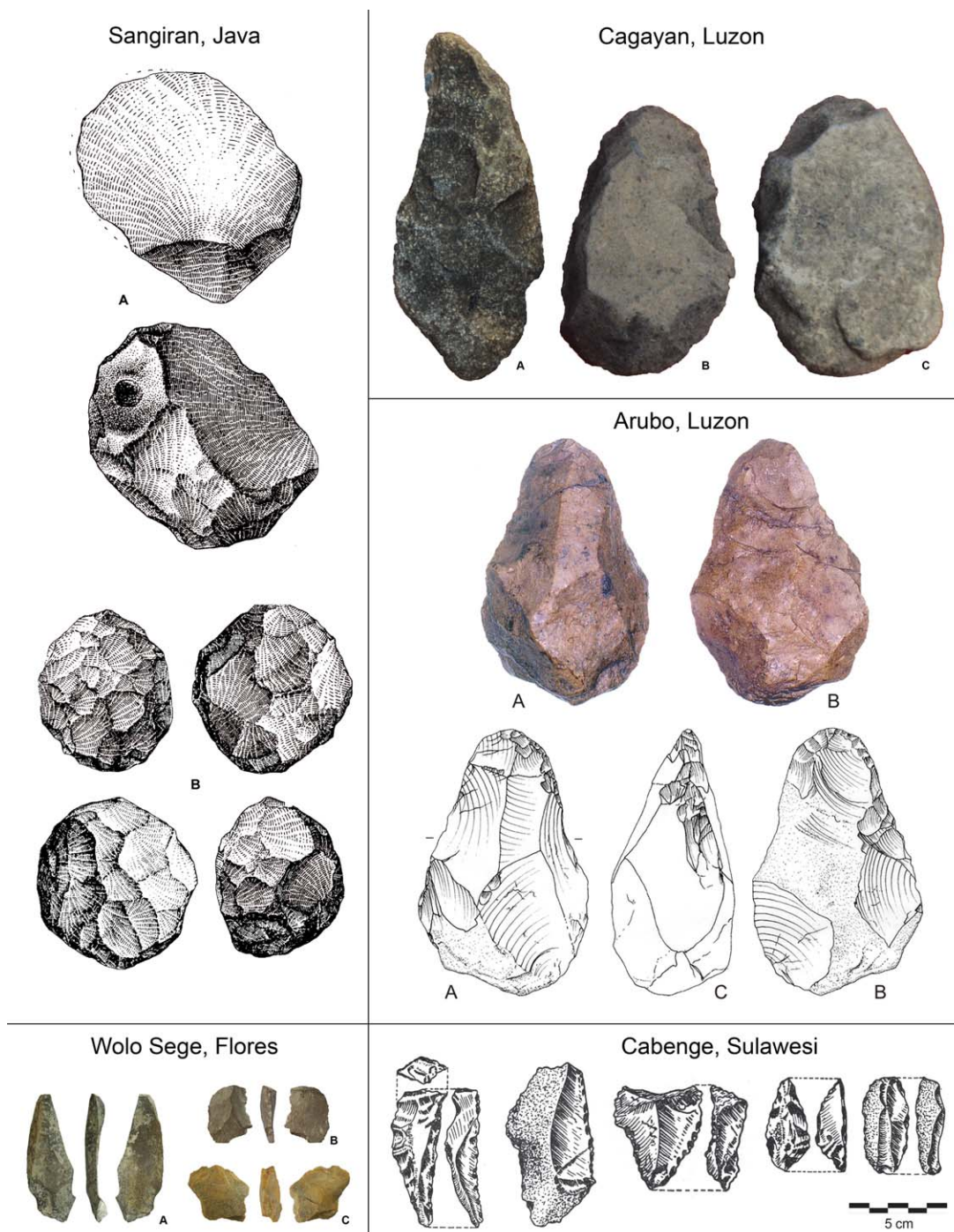


Figure 5. ISEA Early Pleistocene lithic artifacts. Ngebung 2, Sangiran, Solo Basin, Java: A, retouched large flake; B, polyhedron (courtesy of F. Semah).⁶⁶ Cagayan Basin, Luzon, Philippines (photograph: R. Ciochon). Arubo, Luzon, Philippines: bifacially retouched large flake (courtesy of E. Z. Dizon).⁹⁷ Wolo Sege, Soa Basin, Flores: small flakes (courtesy of A. Brumm). Cabenge, Walanae Basin, Sulawesi: small flake tools (modified after H. R. van Heekeren).⁵² (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

address the Middle Pleistocene record for Sangiran and Soa, as well as other areas. Table 2 shows the events, sites, lithics, and fauna that were present during the early Middle Pleistocene.

Sunda

Ngebung (Sangiran)

On Sangiran's northwest flank, the Ngebung Hills lie some 3 km NNW of the Sangiran and Bapang Formation

type sites. The terrain is a dissected escarpment ranging from Quaternary terraces atop the Pohjajar Formation down through the Bapang to the Sangiran Formation. From 1989 to 1994, a French-Indonesian team excavated

TABLE 2. Mid-Pleistocene Transition Synoptic Chart

MIS	start ~ka	end ~ka	events	age ka	Java			Flores			Luzon/Bose			trends
					sites	lithics	<i>Stegodon</i>	sites	lithics	<i>Stegodon</i>	sites	lithics	<i>Stegodon</i>	
11	420	360	MBE	420										ISEA shift to cave occupation/preservation
12	480	420												tropical rainforest
13	520	480	Gunung Sewu uplift & karst formation											New Guinea & Australia
14	580	520												
15	630	580												In following interglacials: shift to more modern forests with reduced diversity
16	680	630												Tibet Plateau min forest
19	800	680	Brunhes-Matuyama	778								Arubo	LFA?	
20	800	800										Kobatu	radial cores	<i>S. luzonensis</i>
21			Oldest Toba/Tektitites	803								Boa Lesa	radial cores	Bose bifaces
22	880	870										Mata Menge	radial cores	<i>S. florensis</i>
23	880	880	EPR	880										Tibet Plateau frigid glacial
24	975	920	Jaramillo	990										Hequing shift to cold

Box 4. Long Chronology

During 125 years of ISEA paleontological research, an early hominin chronology has been difficult to resolve. The most productive research area has been Sangiran, in Central Java, Indonesia. With a thick volcanoclastic sedimentary sequence presenting at many locales, Sangiran has produced a great majority of the region's *Homo erectus* fossils, archaeological sites, and chronological interpretations. It is worth summarizing the evolution of chronological frameworks at Sangiran.

A micro-paleontological Plio-Pleistocene (current early Pleistocene) chronology was established for Sangiran well before WWII.^{228–230} After the war, a reinterpretation of the evidence suggested that the fossils belonged to, in current terms, the late Early-early Middle Pleistocene (~1.0 to 0.4 Ma).^{84,231–235} However, new microfossil analyses done in the 1970s strengthened the initial 'long

chronology.'^{236–238} Alternatively, the first widespread radiometric analyses, based on counting fission tracks, yielded young and highly scattered dates.^{21,239–241} Since the 1980s, a growing number of ⁴⁰Ar/³⁹Ar dates and continually refined sampling schemes have generally shown Sangiran's hominin-bearing sequence to have begun more than 1.5 Ma, possibly as much as 1.86 Ma.^{19,20} Similar chronological debates have been seen for Arc locales, including Flores, Luzon, and Sulawesi.

The long chronology suggests that early hominins arrived in Sunda (Sangiran) in the form of *Homo erectus* before 1.5 Ma. An early form arrived east of Wallace's Line, to Flores, about 1.1 Ma. In the Late Pleistocene, the probable ultimate survivors of these early dispersals are found on Java (Ngandong *Homo erectus*, ~125 ka),¹⁴¹ Flores (*Homo floresiensis*,

~60 ka),¹⁸⁴ and Luzon (*Homo sp. indet.*, ~67 ka).¹⁵⁶

Marine Isotope Stages

The global MIS provide a calibrated environmental framework relating to basic ISEA habitat change. The MIS system uses oxygen isotope levels to indicate alternating warm and cool periods during the Quaternary Ice Age or Pleistocene. Isotope data are drawn from pollen and foraminifera remains in sea-bottom sediments. Deep-sea core sediments also preserve paleomagnetic reversals that can aid in establishing chronology. ISEA deep-sea cores also contain air-fall tephra from volcanic eruptions and microtektites from the Australasian Tektite Strewnfield (Box 5). When subjected to radiometric age analysis, these horizons can be used to refine regional chronology.

at Ngebung 2, where several meters of Bapang riverine sands and gravels overlie the Grenzbank Zone.⁶⁶ Five stratigraphic ensembles yielded stone artifacts and a highly fragmented fauna.⁶⁶ ⁴⁰Ar/³⁹Ar dates on tuffaceous layer heavy minerals produced ages of ~800 ka.⁶⁷ Our own analysis gave an age of 900 ka.⁶⁸

The 2,000+ fossil bones and teeth include more than 800 mammal fossils assigned to species: large bovids comprise 45%; smaller cervids, 18%; and stegodons 8%.⁶⁹ Endemic species include stegodon (*Stegodon trigonocephalus*) and bovid (*Duboisia santeng*). Mainland forms include pygmy hippo (*Hexaprotodon sivalensis*), buffalo (*Bubalus paleokerabau*), rhino (*Rhinoceros sondaicus*), and pig (*Sus brachygnathus*).

Bone surfaces are highly eroded. There are no cutmarks present, but bovid long bones appear to have been intentionally broken and defleshed. Some *Stegodon* tusks are broken as if to create ivory flakes.⁶⁹ The large mainland forms, *Bubalus*, *Rhinoceros*, and *Sus*, should repre-

sent migrants contemporary with the initial *Homo erectus* dispersal. Most of these foraged in open settings but, for rest, depended on closed habitats. The fauna may therefore reflect a forest fringe setting.⁷⁰

Ngebung stone artifacts feature large flakes (including Kombewa type), polyhedrons, cores, cleavers, and hammer stones with little lithic debitage (Fig. 5).⁷¹ Spheroids are recorded from an erosion zone in a lower stratigraphic unit (ensemble A); these could be more recent intrusions.⁶⁶ Ngebung flakes, tools, and spheroids are made on andesite pebbles and cobbles,⁷² likely quarried from Bapang-era erosion surfaces in the Lower Lahar Unit.²³

The Ngebung assemblage has two possible origins (Box 3). On one hand, the biface and cleaver elements recall the Large Flake Acheulean (LFA).^{73,74} Should these be true LFA artifacts, Ngebung would be among the oldest such sites outside of Africa.⁷¹ On the other hand, the Ngebung assemblage resembles ISEA flake industries defined on surface

collections, such as the Sangiran and nearby Pacitanian industries.^{53–55,75} It is possible that some or all of the stone artifacts at Ngebung are surface intrusions from a later period.

Eastern Island Arc

Soa Basin, Flores (Indonesia)

About 0.9 Ma, local volcanic eruptions contributed heavily to Ola Bula basin infill. The earlier volcanic tuff-dominated facies grades upwards into a sandy interval dominated by fluvio-lacustrine tuffaceous sand layers.⁴⁷ At this time, the earlier Pleistocene dwarf stegodon (*Stegodon sondaari*) of Tangi Talo is not represented, but appears to have been replaced by a large-bodied form (*Stegodon florensis*).^{76,77} *S. florensis* likely dispersed from a larger landmass during MIS 22, the first extreme glacial period of the Pleistocene. The accompanying sea-level lowstand certainly opened dispersal routes from Sunda to the Arc and across the Arc. In such conditions,

Box 5. Pleistocene Catastrophes

Three region-wide catastrophes are visible in the ISEA early hominin archeological record. The Australasian Tektite Impact Event produced the widespread Australasian Tektite Strewnfield. Cambodia's Tonlé Sap, the largest freshwater lake in Southeast Asia, may represent the impact crater (Fig. 1).²⁴² Age for the Australasian Impact is estimated at 0.8 Ma, based on ⁴⁰Ar/³⁹Ar and fission-track analysis of individual tektites.^{243–247} Corroborating evidence comes from the position of microtektites in deep-sea cores, always below indications for the Brunhes-Matuyama geomagnetic reversal of 0.78 Ma.^{248–250} Australasian tektites are known in association with early hominin artifacts and mammalian fauna in various contexts, including the Bose Basin, Guangxi, China, and the Cagayan Basin, Luzon, Philippines. In

Bose, the Australasian event may have caused widespread, devastating forest fires which early hominins adapted to through the use of bifacial stone tools.²⁴⁷ The association of stone tools and tektites in Bose is, nevertheless, in debate.^{251,252}

The Toba caldera of northern Sumatra is earth's largest Pleistocene-age volcanic complex. Two of numerous eruptions produced the Oldest Toba Tuff (OTT) and the Youngest Toba Tuff (YTT). New research suggests that OTT represents a total tephra volume of 2,300 cubic km,²⁵³ which is comparable to the better-known YTT total volume of 2,800 cubic km.¹⁴⁹ The Australasian Strewnfield and OTT are closely related in time. At ODP site 758, northwest of Toba, Australasian microtektites and OTT are associated in ash layers D and E.²⁵⁴ YTT is

found in undersea deposits across the Indian Ocean, as well as the Arabian and South China Sea.²⁵⁵ YTT dates to about 73,500 years \pm 3,000 years¹⁴⁸ or 73,000 years \pm 4,000 years ago.¹⁴⁹ YTT has been implicated in initiating the last glacial cycle due to its coincidence with not only ice buildup during this time,²⁵⁶ but population bottlenecks of Neanderthals in western Eurasia and *Homo sapiens* in Africa.^{257,258} However, the arguments are weak. YTT traces have not been identified at ISEA fossil hominin sites. The Middle Solo sites and Liang Bua appear to predate the event and the Callao stratigraphy apparently postdates YTT. Given the present state of knowledge, it seems that across ISEA the YTT event did not generate significant bottlenecks or extinctions among mammalian populations.^{259–261}

larger-bodied stegodons could have dispersed to formerly small landmasses where dwarf species could have been overwhelmed.

Mata Menge, Boa Lesa, and Kobatuwa. These three stratified sites lie in the sandy interval above Wolo Sege and Tangi Talo (Fig. 3B).⁴⁷ Mata Menge has a basal date of \sim 880 ka. Boa Lesa and Kobatuwa lie up-section from Wolo Sege and Tangi Talo. A series of tuffs runs through the entire sequence. Fission track dates for capping sediments place them at \sim 700 ka. Among the three sites, major faunal elements include large-bodied stegodon (*Stegodon florensis*), Komodo dragon (*Varanus komodoensis*), giant rat (*Hooijeromys nusatenggara*), and giant tortoise (*Geochelone*). The large stegodon on Flores is somewhat smaller than the large form on Java.⁷⁷

With a total of 507 stone tools, Mata Menge has the largest early hominin archeological assemblage in ISEA.⁷⁸ Lithic resources were brought to the site in the form of flake blanks. The more complex tools show a reduction sequence based on centripetal or radial removals on the

blanks (Box 3). The Acheulean-like elements of Wolo Sege are not present at Mata Menge.

The Soa Basin Ola Bula formation, from Wolo Sege to Mata Menge, has ISEA's most complete archeological record. Wolo Sege indicates hominin arrival at more than 1.0 Ma. The change in fauna between Wolo Sege and Mata Menge demonstrates an EPR-related faunal turnover at about 900 ka. After this turnover, the Soa Basin shows phylogenetic continuity in large-bodied animals until the arrival of *Homo sapiens* at 12 ka.⁴⁷

Southern Wallacea Outer Arc (Indonesia)

South of Flores, the Savu Basin subduction trench ranges to more than 3,000 m in depth (Fig. 8). Sumba and Timor lie on the basin's southern arc. At the lowest Pleistocene sea-level lowstands, overwater channels of 20–40 km separated these islands from Flores. Both islands have sites at which Paleolithic stone artifacts and Pleistocene vertebrate fossils are found in physi-

cal proximity. Nevertheless, age and relationship remain unclear.

Talau basin (Timor). Pleistocene fluvial conglomerates are exposed along the Talau River border between Indonesian Timor and East Timor. During the 1950s and 1960s, localities east and south of Atambua (Indonesian Timor) produced *in situ* fossils and surface stone tools.^{79,82,84} Taxa included *Stegodon timorensis* (pygmy stegodon), *Geochelone* (giant tortoise), and *Varanus komodoensis* (Komodo dragon).^{80,81,83,86} During the 1990s, fauna and artifacts were associated at two more sites, but accounts remained preliminary.⁸⁷ In 2015, at Raebia, east of Atambua, the Iowa-Bandung project located stegodon, giant tortoise and possible stone artifacts in relation to bracketing tuffaceous lenses. Nearby, at Sadi laun, stone artifact clusters were excavated from deflated terrace deposits.

Noelbaki (Timor). At Timor Island's west end, near Kupang, Paleolithic stone artifacts appear in coarse fluvial gravels cut through by modern

watercourses. In 1978, Soejono surveyed at Noelbaki and Noeltarus, reporting choppers, chopping tools, flakes, blades, and proto-hand-axes made from large flakes.⁸⁸ In 2015, at the same localities, the Iowa-Bandung project differentiated a laminar industry with limited patina from large flake tools with heavy patina. Contextual materials are in analysis.

Watambuka and Lewapaku (Sumba). On Sumba's northeast shore, Watambaku lies in current estuarine contexts. In 1978, a stegodon left mandible (*Stegodon sumbaensis*) was recovered without context.^{89,90} In 2015, the Iowa-Bandung project found two retouched chert flakes in depositional contexts indicating lower (Pleistocene) sea level. In 2012, at Lewapaku, 30 km inland, the Wollongong-Bandung Geological Museum project found, *in situ*, tusk fragments, a tooth (*Varanus komodoensis*), a giant murine rodent (?*Hooijeromys*), and a bird long bone. A loose comparison was made with the fauna of Tangi Talu.⁹¹

Luzon (Philippines)

The Philippine archipelago has early hominin evidence northernmost on the Arc and farthest from Sunda. Deep sea channels currently separate the archipelago from other ISEA landmass systems, suggesting the presence of dispersal barriers throughout the Early and Middle Pleistocene.

Paleoanthropological research has a long history on Luzon. During the 1950s, Paleolithic flake tools and extinct fauna were found together in the Cagayan Basin, and probable dispersal routes were hypothesized.⁹² Australasian tektites were also discovered at several locations.⁹³ During the 1970s, researchers at the National Museum of the Philippines surveyed many more Cagayan co-occurrences of stegodon and artifacts.⁹⁴ More recently, fossils of several mammal families have been found in archeological contexts, including small stegodon (*S. luzonensis*), and the tektite association has been confirmed.^{95,96} Recent research also suggests that the Luzon Middle

Pleistocene flake tool assemblages fit within the Large Flake Acheulean.⁹⁷

Cagayan Basin. At Luzon's northern end, the Cagayan Basin is a 250 x 80 km subduction zone feature with 10 vertical km of sedimentary infill (Fig. 3C). The upward-coarsening volcanics reflect the tectonic and volcanic evolution of the adjacent Cordillera Central volcanic arc. The upper 900 m comprises two formations of interbedded fluvial and pyroclastic deposits, the Ilagan (lower 500 m) and the Awidon Mesa (upper 400 m). The sequence consists of four depositional environments: meandering stream, braided stream, lahar and pyroclastic flow, and ash-fall deposits.⁹⁸ Cagayan has scores of localities with stone tools and, in some cases, tektites and Pleistocene fauna.⁹⁹ Field work has recently been resumed in the Cagayan Basin where the contemporaneous occurrence of stone tools, tektites, and Pleistocene faunas has been confirmed.¹⁰⁰

Enrile Southern Quarry. An important Awidon Mesa formation locality is Southern Enrile Quarry, near Peñablanca. Here, a Danish-Australian team is bracketing the fossil and artifact-bearing level using ⁴⁰Ar/³⁹Ar on volcanic elements and luminescence on low-temperature sediments. Preliminary ⁴⁰Ar/³⁹Ar ages range from the late Early and Middle Pleistocene to 0.4 Ma as the secure youngest age.¹⁰¹ It is reasonable to entertain an Early Pleistocene Revolution (EPR) time frame for the artifact-fauna-tektite association.

Arubo Basin. Approximately 300 km south of Cagayan, Arubo is a complex of open sites in the Sierra Madre foothills of Central Luzon.¹⁰² A morphologically heterogeneous lithic assemblage has been collected here, primarily from sites out of geological context.⁹⁷ The site complex lies close to a chert boulder deposit, which served as the raw material source. The stone tool assemblages include the Large Flake Acheulean (LFA) hallmarks of bifaces, cleavers, flake cores, retouched flakes, and choppers (Fig. 5). Microscopic use-

wear analyses suggest curation and reuse.^{103,104} The Arubo complex age remains unknown, but is likely to be correlative with the LFA features at the Cagayan sites.

The *Stegodon*-artifact-tektite (Box 5) association at Awidon Mesa Formation is crucial for understanding Luzon early hominin arrival (Fig. 5). This association suggests that early hominins arrived at Luzon by 800 ka, probably bringing LFA technology. It remains to be seen whether or not the Luzon dispersal relates to the Soa Basin Middle Pleistocene faunal turnover. It must be noted that in the Cagayan and Arubo Basins, the Middle Pleistocene stone technology is not easily differentiated from the Tabonian industries of the late Upper Pleistocene found on Palawan Island, which are associated with *Homo sapiens*.⁹⁴

MID-BRUNHES EVENT OR LATE MIDDLE AND LATE PLEISTOCENE

MIS 12/11 (~480-360 ka) began a new pattern within the 100-kyr climate cycle. Glacial phases became long (70-90 ka) and very cold, while interglacials became short (10-30 ka) and warmer.¹⁰⁵ This transition, the Mid-Brunhes Event (MBE), began the four large-amplitude glacial-interglacial cycles that have structured global climate to the present.¹⁰⁶ With MBE, earth's climate became more orderly, predictable, and extreme.¹⁰⁷

MBE had significant global consequences. MIS 12 exhibited severe cooling effects.^{108,109} MIS 11 marked the longest, warmest interglacial, with sea level rising to 20 m above the present highstand.¹¹⁰ The MBE 12/11 complex probably aided in both dispersing and isolating ISEA large mammals. It is worth noting that in western Eurasia, the appearance of Neandertal traits is correlated with the onset of MIS 11.¹¹¹ Extreme interglacial sea level highstands also came during MIS 9 and 5e.

On mainland China, in conjunction with MBE, the Hulu and Dangge cave flowstones record the beginning of monsoon rainfall. The flowstones record the dry monsoons directly associated with the commencement of massive periodic

TABLE 3. Mid-Brunhes Event Synoptic Chart

MIS	start ~ka	end ~ka	events	age ka	Java & (Malaysia)			Flores			trends
					sites	lithics	Stegodon	sites	lithics	Stegodon	
1	12										
2	28	12	Flores eruptions	17							Holocene
3	62	28									
4	74	62	Youngest Toba	73	(Lenggong)	flakes					
5	120	74			Ngandong	flakes	<i>S. trigonocephalus</i>	Liang Bua	radial cores	<i>S. florensis</i> <i>S. insularis</i>	MIS 5-2: ITCZ placement for SE Monsoon. Dry conditions throughout ISEA Last interglacial; high sea levels
5e	130	120									Liang Bua sedimentation
6	190	130									
7	250	190									
8	300	250			Song Terus	flakes (Pacitanian?)	<i>S. trigonocephalus</i>				drying in New Guinea & Australia
9	340	300									Song Terus sedimentation
10	360	340									high interglacial sea levels
11	420	360	MBE	420							severe cooling 100-kyr obliquity cycle; cold glacials (70-90 ka); warm interglacials (10-30 ka)

North Atlantic glacier ice calving known as Heinrich events.^{112,113} These events produced cold winters in Europe and dry monsoons in China.^{114,115} Another consequence of Heinrich events was the southward shift of the Tropical Rain Belt.¹¹⁶ The sequence of events, stretching halfway around the globe, indicates the swiftness of glacial climate change.

The Mid-Brunhes Event marked yet another significant change in regional erosion and sedimentation patterns. Some Miocene limestone massifs developed karst landscapes. Central Java's Southern Mountains Miocene coral beds (Gunung Sewu) provide an example. At Punung III in Gunung Sewu, a U-series age of 492 ± 38 ka for the lower flowstone provides a minimum age for uplift.¹¹⁷ This determination corroborates other Middle Pleistocene uplift estimates relating karst development in the Southern Mountains.¹¹⁸⁻¹²⁰

Early hominins found shelter in these newly opened caves. The Song Terus cave fluvial stage documents the accumulation of stone artifacts before 300 ka. Liang Bua opened for infilling about 195 ka and shows evidence of hominin habitation shortly thereafter. The evolution of Callao cave is not yet clear.

The Mid-Late Pleistocene boundary (MIS 5e, 130-120 ka) was a globally important climatic event, represented in Paleolithic sites across northwestern Eurasia. However, sedimentary sequences in Southeast Asia do not seem to register the Last Interglacial in significant ways. One Late Pleistocene catastrophe, the Youngest Toba Eruption, is not identifiable in sedimentary sequences throughout ISEA (Box 5). Table 3 shows the events, sites, lithics, and fauna present during the Mid-Brunhes Event, late Middle Pleistocene, and Late Pleistocene.

Sunda

Trinil, Java

Recent observations from Dubois' historical faunal collection at the Netherlands Museum in Leiden⁴⁶ suggest that *Homo erectus* may have

occupied Trinil during the Middle Pleistocene, displaying advanced cognition and cultural behavior. Within the collection, the *Pseudodon* shell assemblage represents adult large-sized specimens (80-120 mm in length) from varied riverine settings. This suggests that individual shellfish were selected for consumption based on large size. One shell valve shows signs of modification by retouch, possibly resulting from use as a cutting or scraping tool. Another shell displays a zigzag pattern of grooves on the central part of the left valve. The marks are attributed to the engraving of meaningful abstract patterns on an attractive substrate.¹²¹ In other words, Trinil hominins are thought to have intentionally marked the shell.

Luminescence and ⁴⁰Ar/³⁹Ar analysis on the shells' adhering sediment give a maximum of 0.55 Ma and a minimum of 0.44 Ma,⁴⁶ or about half the age estimate based on analysis of the associated mammalian fauna.⁴⁴ This new age would seem to pull Trinil away from the Sangiran fossils and an early Middle Pleistocene Ngebung cultural affiliation. Should the shell marking prove factual, does it indicate cognitive abilities expectable in the later Java sites in the Song Terus karst and the Middle Solo Terraces? On date alone, it is tempting to draw a comparison with mid-Middle Pleistocene early hominin dentognathic fossils from Hexian, eastern China, and Penghu, Taiwan. Trinil at a mid-Middle Pleistocene age may represent a time in which *Homo erectus* diverged in several regional contexts.

The Dubois collection zigzag shell could represent part of a regional trend toward early hominin cultural diversification. Nevertheless, the Trinil shell marking has a complexity normally associated with early Late Pleistocene *Homo sapiens* in Africa.^{122,123} It is possible that diversifying Middle Pleistocene *Homo erectus* had similar cognitive ability, but the find is unique. The problem remains that the Trinil *Hauptknochenschicht* is a complex deposit, apparently a mixed sequence of flood-borne overbank accumulations. Bones, shells, and sediments of var-

ied chronology may have merged in this context.¹²¹ Given the poorly known nature of the site and the primitive morphology of the Trinil calotte, we hesitate to grant advanced symbolic behavior to the group represented by the calotte.

Gunung Sewu, Java

The Southern Mountains of East Java lie on the Indian Ocean coast, 100-150 km south of the Solo Basin. The area has been of geological interest since the 1830s and of archeological interest since the 1930s.¹²⁴ In 1935, von Koenigswald and Tweedie collected a range of flake and pebble tools from the Baksoka riverbed, later described as the Pacitanian industry.¹²⁵ Since the 1990s, Gunung Sewu research has focused on cave and rock shelter habitations and the use of local lithic resources, including chert, jasper, limestone, and meta-limestone.¹²⁴ Gunung Sewu stone sources may have provided the raw materials for Sangiran sites such as Ngebung.

Song Terus. Most Gunung Sewu caves have yielded Late Pleistocene and Holocene deposits, but one, Song Terus, features an important Middle Pleistocene infill. In 1953, Soejono and Basuki excavated fauna and an archeological industry involving stone, bone, and shell.⁵² In the late 1990s, an Indonesian-French team excavated more than 15 m of stratigraphy in two units.¹²⁶ The lower unit consists of flood alluvium from the 12-m terrace. The layers contain fauna (rhinoceros, tapir, and cervid) and flake tools.^{85,126} Combined U/Th-ESR analysis indicates that the lowest archeological levels arrived ~300 ka.¹²⁷ The flake tools may relate to classical Pacitanian lithics (Fig. 6).¹²⁶ The fluviially derived archeological deposits increase in density after 180 ka. By 80 ka, the local stream at Song Terus had entrenched below the cave entrance and a more typical cave infilling took over. Archeological remains include hearths and fauna, but few lithics. This seems to represent sparse inhabitation and may be

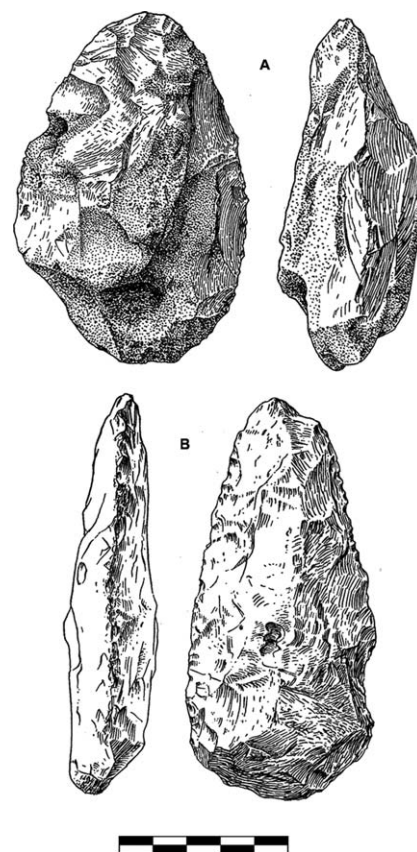


Figure 6. Two bifaces from the Baksoka valley, Gunung Sewu, Java (modified after G.-H. Bartstra).¹²⁵

indicative of waning Sunda *Homo erectus* populations.¹²⁶

Other Gunung Sewu caves, such as Song Klepek and Braholo, aid in understanding late *Homo erectus* lithic technology and landscape use, and may eventually shed light on the terrace lithic industries such as the Pacitanian and Sangiran Flake Industry. The deep Gunung Sewu caves may be especially important for understanding hominin adaptations during MIS 6 (150-130 ka), when the Southeast Asian mainland was exceptionally cold and dry. At this time, the equatorial insular province may have served as an early hominin refuge.

Middle Solo Terraces, Java

As the Solo River cut through the Kendeng Hills, it entrenched within Pleistocene terraces. In 1931, Geological Survey of the Netherlands geologist Carel ter Haar discovered a bone bed near the base of the Solo River

TABLE 4. Sambungmacan-Ngawi Calvaria Sites

Village	Location	Date	ID	Anatomy
Poloyo	–	1973	Sm 1	calvaria
Poloyo	–	1973	Sm 2	tibia fragment
Mlale-Cemeng	4 km upstream from Poloyo	1977	Sm 3	calvaria
Mlale-Cemeng	4 km upstream from Poloyo	2001	Sm 4	calvaria
Selopuro	6 km downstream from Trinil	1987	Ngawi 1	calvaria

20-m terrace. Ngandong sat on the cutbank of an acute river bend within the Kendeng Hills. From 1931 to 1933, the Survey excavated the bone bed within a volcanoclastic sand stratum.^{128–130} Ngandong produced 12 “Solo Man” cranial remains.

Since the early 1970s, four Ngandong-like calvaria have been found 15–20 km upstream from Ngandong, a few kilometers upstream from the Trinil locality. The calvaria are chance finds in the eroding Solo River bank; the sedimentary details of their provenance are as yet unknown. As a series, the fossils are generally called by the names of their administrative municipalities, Sambungmacan–Ngawi,

and are more specifically identified by the three villages nearest their find spots (Table 4).

Middle Solo cranial morphology. Compared to Sunda Early Pleistocene *Homo erectus*, the Sambungmacan–Ngawi specimens show derived features, including a relatively horizontal supraorbital torus that thickens laterally, continuous supra-orbital/supramastoid crests, and a well-defined occipital torus and superior nuchal line.¹³¹ Cranial walls are relatively tall and the coronal profile is “roundedly tent-shaped.”¹³¹ Cranial capacity is increased.^{131–133} The series exhibits minor postmortem distortions or surface erosion.

The Ngandong hominins range from cranial vault fragments to a nearly complete calvaria retaining delicate ethmoid and sphenoid structures.¹³⁴ The Ngandong calvaria are larger and more robustly built than the Ngawi–Sambungmacan series (Fig. 7). The lateral walls of the braincase are more vertically oriented, helping cranial capacity range upward to 1,250 cc. Raised temporal lines on the cranial vault give a puffy appearance to the vault when viewed from the front. The strongly developed supraorbital torus does not form a continuous bar, but rather meets in the glabellar region in a distinct depression. The pronounced occipital torus has greater rearward projection.¹³¹

Ngandong taphonomy. The 1930s excavations produced ~25,000 vertebrate fossils, including at least 10 terrestrial mammals: buffalo (*Bubalus*), cattle (*Bibos*), deer (*Cervus palaeojavanicus*), hippopotamus (*Hexaprotodon*), leopard (*Panthera pardus*), muntjac (*Muntiacus*), pig (*Sus terhaari*), rhinoceros (*R. sondaiensis*), stegodon (*S. trigonocephalus*), and tiger (*Panthera tigris*). Bovids represent more than half of the assemblage.¹³⁵ Broken and disarticulated elements greatly outnumbered well-preserved specimens and partially articulated skeletons. No cut marks have been reported and few verifiable artifacts appeared in excavation.

Recent excavations have isolated the extent of the 1930s excavation and located the bone bed stratum within. The *Homo erectus* specimens can now be placed surely within the original facies C of the basal fossiliferous horizon.^{130,134,136} Bone bed sedimentary dynamics are also under investigation. The deposit, comprising poorly sorted, high-energy fluvial sand and gravel, shows hyper-

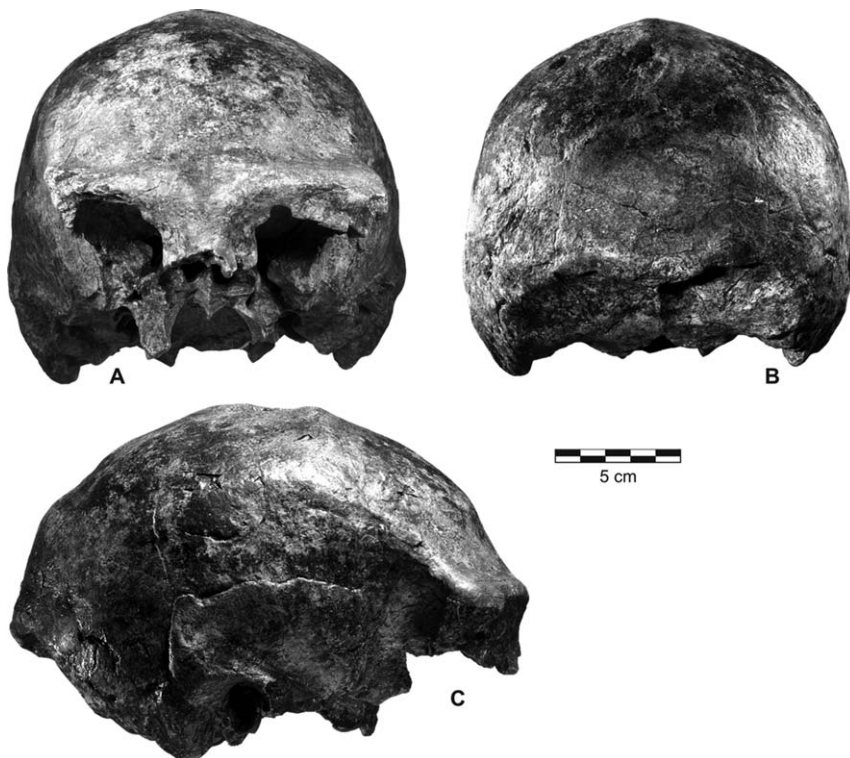


Figure 7. *Homo erectus* calvaria (Solo Skull V, Ng 6): Ngandong, Middle Solo Valley, Java, Cranial capacity: 1,251 cc.²⁷⁵ Courtesy of the American Museum of Natural History, New York.

TABLE 5. Middle Solo Terraces Historical Ages Analyses

Year	Methodology	Age
1939	Von Koenigswald attributes the Ngandong 1930s excavation fauna	Upper Pleistocene ¹³⁷
1988	U-series on Ngandong bone fragments	~165 ka ¹²⁹
1996	ESR/U-series on bovid teeth from the Ngandong 1930s excavation area	53-27 ka ¹³⁸
2007	luminescence and U-series on Punung fauna breccias*	128 ± 15 to 118 ± 3 ka ¹¹⁷
2008	gamma-ray spectrography on Ngandong/Sambungmacan hominin fossils	70-40 ka ¹³⁹
2011	40Ar/39Ar incremental heating & ESR/U-series on Ngandong and Jigar fauna	546.6 ± 12 ka ¹⁴⁰
	ESR/U-series	min age: 143+20/-17 ka ¹⁴⁰
2014	red thermoluminescence (red TL) on Ngandong bone bed fluvial sediments	~130-102 ka ¹⁴¹

concentrated flow features typical of a lahar event. The volcanoclastic source appears to be an andesitic cone located about 50 km away.¹³⁴

With this new information, a taphonomic hypothesis can be sketched, its events including upstream multi-species aggregation, mass death and relatively speedy carcass decomposition, and mass flow of osseous elements downstream to concentration and burial at Ngandong. The aggregation may have been caused by drought or volcanic eruption; mass death may be related to localized ash fall. During lahar transport, the carcasses were disarticulated and individual bones broken, but surfaces and edges were not eroded.¹³⁴

Middle Solo Terraces Ages. The age of the 20 m terrace sediment constituents is yet to be resolved. The historical sequence of age analyses is presented in Table 5.¹³⁷⁻¹⁴¹

The oldest dates push these fossils back into the Middle Pleistocene. The youngest results (53 ka – 23 ka)¹³⁸ straddle the 47 ka arrival threshold for *Homo sapiens* to ISEA and Sahul. The youngest dates suggest that *Homo erectus* survived the arrival of *Homo sapiens* for a significant time. It is reasonable, nevertheless, to reject the earliest and latest ages as anomalous. The bulk of the ages suggest that the hominins at Middle Solo terraces generally relate to the Last Interglacial (MIS 5e), falling just before, during, or just after. The general consensus is that the Middle Solo terraces represent the latest form of ISEA *Homo erectus*.¹⁴⁰ The question is open as to whether or not arriving *Homo sapiens* encountered *Homo erectus* of the Ngandong type.¹⁴²

Lenggong Valley, Perak (Peninsular Malaysia)

Since the 1930s, several Lenggong Valley localities have produced simple stone tool assemblages collectively known as the Tampanian.¹⁴³ As surface finds, the Tampanian was thought to be an early hominin technology similar to the Pacitanian.¹⁴⁴ The site of Kota Tampan is one of several localities that show a tuffaceous stratigraphy without faunal preservation. Evidence is now conclusive that the site lies within the Youngest Toba Tuff (YTT).¹⁴⁵⁻¹⁴⁷ YTT dates to about 73,500 years ± 3,000 years¹⁴⁸ or 73,000 years ± 4,000 years ago (Box 5).¹⁴⁹ Other excavated Lenggong sites are stratigraphically younger. One much younger site includes a *Homo sapiens* skeleton.¹⁵⁰

The Lenggong Valley sites and the Tampanian are difficult to place in human biogeographic context. The YTT date puts Kota Tampan within the realm of possibility as an early hominin site; however, the stone technology associated with the site could represent either early hominins or modern humans. The YTT date has been used as evidence of a pre-YTT eastward dispersal of *Homo sapiens*.¹⁵¹

Eastern Island Arc

Wae Racang Karst, Flores

On northwestern Flores, the Manggari limestone massif (Miocene age) extends more than 500 m above sea level (Fig. 3B). The local karst system began developing about 600 ka as the Wae Racang River incised more than 100 m into the massif. Five river terraces record this evolution. The Liang Bua cave site is the result

of the river exposing, then invading the karst system. The river now lies 30 m below and 200 m distant from the cave.⁵

Liang Bua. The cave is 14 km north of Ruteng and 25 km from the north coast. Stone artifacts began accumulating at about 190 ka. After 100 ka, channel erosion created relief within the soft debris. Remnant areas of higher ground later became a focus for hominin habitation from 74–61 ka.¹⁵² There is no direct indication of YTT in the cave sediments. The Liang Bua archeofauna sequence ranges from ~95 ka to the present.^{153,155} Recently, a depositional hiatus has been identified between ~60 and ~17 ka.¹⁵³

The Liang Bua archeofauna consists of unfossilized but well-preserved mammal, bird, reptile, and mollusk remains. The pre- and post-hiatus assemblages are distinct in species representation. For the early sequence, that associated with *Homo floresiensis*, large vertebrates include giant tortoise (*Geochelone*), three giant rat species (*Papagomys*, *Spelaeomys*, or *Hooijeromys*), and Komodo dragon (*Varanus komodoensis*). A similar faunal association is seen at the Soa Basin sites about 700,000 years earlier. However, Liang Bua uniquely preserves a very small stegodon (*Stegodon florensis insularis*), thought to be the dwarfed descendant of the large-bodied EPR-arrival, *Stegodon florensis*, as well as a diminutive hominin (*Homo floresiensis*).¹⁵³ The origin and unique morphology of *Homo floresiensis* has been the subject of numerous interpretations (Box 6).

Excluding the hominin fossils, the Liang Bua fauna is characterized by phylogenetic continuity and low

Box 6. *Homo floresiensis* Skeleton

The Liang Bua skeleton (LB1), the smallest known fossil hominin, expresses a mosaic of primitive and derived features that are absent in other early hominin groups.²⁶² Fragmentary remains have been recovered from at least nine individuals.^{263,264} Our description of *Homo floresiensis* is based on partial skeleton LB1 and mandible LB6. LB1 exhibits a marked reductive trend in its facial skeleton, with extremely small overall cranial size, a primitive low and anteriorly narrow vault shape with thin cranial bones, a relatively prognathic face, and small teeth.¹⁸⁴ Nevertheless, the mandibles of *Homo floresiensis* (LB1 and LB6) are buttressed, as seen in the holotype of *Homo habilis* (OH7).²⁶⁵ The postcranial skeleton exhibits some primitive features, including flared hipbones; short collarbone; forwardly positioned shoulder

joint²⁶³; shortened femur and tibia; trapezoid, scaphoid, and capitate wrist bones that are primitive and resemble those of *Homo habilis* (OH8)²⁶⁶; and a foot exhibiting primitive features including long lateral toes, a short hallux, and the absence of a well-defined medial longitudinal arch, resulting in flat feet.²⁶⁷ The only relevant wrist element known for *Homo erectus* in either Africa or Asia is one damaged lunate from Zhoukoudian.²⁶⁸ It is therefore impossible to compare the LB1 wrist morphology with that of *Homo erectus*. It is distinctly possible that the wrist morphology of early *Homo erectus* resembled that of *Homo habilis* (OH8), and thus could have been a likely precursor to *Homo floresiensis*. This is more plausible than a proposed transcontinental migration of *Homo habilis*.

A decade after discovery, the evolutionary processes responsible for the small size and unique morphology of the LB specimens are still debated.²⁶⁵ An extreme interpretation relates LB1 to a pathologically dwarfed *Homo sapiens* individual. Jacob and colleagues suggest that LB1 represents a “pygmoid australomelanesian” with developmental abnormalities.¹⁷⁹ Other hypothesized conditions include Laron syndrome,²⁶⁹ cretinism,²⁷⁰ and Down syndrome.²⁷¹ However, LB1 morphology does not definitively reflect any known systemic pathology. Currently, the LB1 stratigraphic context is being reevaluated.⁵⁰ A probable older last occurrence for *Homo floresiensis* at Liang Bua, in excess of 60 ka, would preclude the pathological *Homo sapiens* hypothesis.

species richness, as well as by relatively large and small body sizes. These are features of “impoverished and disharmonic insular faunas” typical of isolated oceanic islands.⁶ Within this context, the *Homo floresiensis* skeleton exhibits small stature, a small brain, relatively long arms, robust lower limbs, and long feet. In sum, *Homo floresiensis* skeletal features resemble those of small-bodied taxa on Flores and across the Arc. Small bodies helped these forms remain successful as long-term members of insular Arc faunas (Box 2).^{6,7}

The early Liang Bua stone technology shows a radial or centripetal reduction sequence similar to that seen at Mata Menge during the Middle Pleistocene.¹⁵⁴ The stone tools are most closely associated with the butchered stegodon remains, primarily dental and skeletal elements of juveniles.¹⁵⁵ Continuity in the stone artifact technology, Mata Menge to Liang Bua (800 kyr), strengthens the image of Flores as an isolated early hominin territory.^{78,154} Archaeofaunal continuity seems to corroborate the trend.

Homo sapiens arrived in ISEA, likely including Flores, by 47 ka. At Liang Bua, nevertheless, modern humans appear after deposition resumes at ~12 ka. The *Homo sapiens* archeofauna sequence has freshwater mollusks, including Thiariidae (*Thiara granifera* and *Melanoides tuberculata*) and Neritidae (*Neritina pulligera*, *Neritodryas cornea*, *Neritodryas dubia*, *Septaria porcellana*, and *Clithon squarrosus*).¹⁵⁵ Modern humans also introduced a range of exotic animals to the island, including the Sulawesi warty pig (*Sus celebensis*) and the Eurasian pig (*Sus scrofa*), long-tailed macaque (*Macaca fascicularis*), Javanese porcupine (*Hystrix javanica*), and masked palm civet (*Paguma larvata*).¹⁵⁵ Only the Komodo dragon (*Varanus komodoensis*), an opportunistic predator and scavenger, is represented throughout the archeofauna sequence.

Cagayan Basin, Luzon

Callao Cave. The Cagayan’s eastern flank has a significant Miocene karst massif (Fig. 3C). In 2003, Armand

Mijares began excavating at the Callao Cave opening.¹⁵⁶ In 2007, a Philippine-Australian partnership expanded the work. The excavation encountered a rich fauna including native brown deer (*Cervus mariannus*; 90% of the identifiable bone fragments), Philippine warty pig (*Sus philippensis*), and an unspecified extinct bovid. Element representation and fragmentation for the cervids indicated that both whole and partial carcasses were brought into the cave for further processing. Some bones show cut marks, but no stone tools were found.⁸

Near the base of the excavated area, Layer 14 yielded a carbonized breccia with relatively dense fauna. Among fragmentary hominin limb bones, the breccias contained a complete third metatarsal. Two cervid teeth from Layer 14 were dated. U-series ablation on one tooth produced a minimum age estimate of 66.7 ka. ESR on the other tooth corroborated the result.⁸ In 2014, further excavation in Layer 14 produced more hand and foot bones and a series of upper teeth. The dentition is of archaic character.⁹

The initial interpretation of the Callao metatarsal went in two directions. The small dimensions and gracile morphology were linked to small-bodied *Homo sapiens*, including modern Philippine Negrito populations. Alternatively, the fossil drew comparison with small early hominin species such as *Homo habilis* and *Homo floresiensis*. The new Callao finds corroborate the early hominin comparison and strengthen the hypothesis for a second colonization east of Wallace's Line. It is tempting to link the origins of these finds with the EPR-age Cagayan Basin dispersal involving hominins, large-bodied stegodons, giant rats, and other insular species. The Australasian Tektite Impact age suggests that such an event would date to at least 800 ka.

Maros Karst, South Sulawesi

Some 80 km southwest of the Walanae sedimentary basin lies the Maros limestone karst system. Here, local stream courses follow intersecting joints to form plateau-like hill masses. In areas of maximum plateau dissection, steep-sided towers are isolated on alluvial plains.¹⁵⁷ The towers have many caves and rock shelters, some of which have prehistoric archeology.

Recent excavations in several caves have exposed cultural levels extending back more than 35 ka. Stone technology is based on small bipolar cores that can resemble very small bifaces. Archeofaunas have small mammals, including monkeys (*Macaca* sp.), bear cuscus (*Ailurops* sp.), and Celebes warty pigs (*Sus celebensis*). Freshwater gastropods (*Tylomelania perfecta*), fish, and birds are also represented.^{158,159} Pigment-based rock art is now dated to 39.9 ka.¹⁶⁰

At one Maros cave, an upper archeological complex ranges back to ~41 ka. Well below, a lower assemblage is quite different. The stone technology is based on minimally reduced cores and retouched cobbles yielding flakes and debitage. The fauna has *Elephas* and *Stegodon* and no smaller species. The levels contain no pigments. The deposits are older than ~53 kyr ago and may

be significantly older. This is a major change in the archeological column. The most economical interpretation is that at ~41 ka *H. sapiens* replaced an earlier population of archaic hominins.¹⁶¹ The cave environments of the Maros karst may represent the best preservation of levels indicating the arrival of *H. sapiens* and the extinction of an as-yet undetermined early hominin population.

DISCUSSION

With basic space and time data in hand, we can turn to basic issues of ISEA early hominin biogeography. Two assumptions guide us. First, early hominins arrived at ISEA as generalized hunter-scavengers integrated within mainland Eurasian mammalian faunas.¹⁶² As such, hominins directly responded to the movements of nonhuman fauna members. Second, within insular contexts, mammalian faunas were particularly sensitive to environmental processes, including dispersal, isolation, vicariance, relict survivorship, and genetic drift. During a million-and-a-half years of shifting ISEA habitats, early hominins responded to many insular opportunities and constraints. Here, we address current issues relevant to the dispersal and isolation of early hominins and their extinction in relation to the arrival of *Homo sapiens*.

Dispersal

Overwater Transit. Even at maximum sea-level lowstands, deep-water channels separated Sunda and Eastern Island Arc landmasses. Heading east from Java, the Lombok and Komodo Straits ranged from 20 to 35 km at maximum lowstands.¹⁶³ Farther north, between Borneo and Sulawesi, the Makassar Strait was never less than 40-km wide. Sulawesi and Flores are separated by a minimum of 60 km of sea with cross-currents (Fig. 8). It is unlikely that a dry-land connection ever existed across the Mindoro Strait to connect Borneo with Luzon via Palawan.¹⁶⁴ Presently, strong north-to-south flow-through currents assist in isolating populations on either side of Wallace's Line.^{165,166} In crossing

overwater to the Arc, Eurasian fauna could have arrived from various Sunda sources via current Java or Borneo.^{32,167}

Alfred Wallace was the first to discuss overwater fauna movements with waif dispersal among the more common means.^{168,169} Waifs are individuals or small groups swept away from one environment and transported by water or air currents to a new territory.¹⁷⁰ Some terrestrial forms, such as stegodon, giant tortoise, and Komodo dragon could float or swim following the prevailing currents. Hominins more likely rafted, either accidentally or purposefully.⁷ Overwater waif dispersal renders unlikely any subsequent gene exchange with the source population.¹⁷¹ Such long-term isolation on small islands is the basis for insular evolution.

Isolation

With the late Early Pleistocene Transition (MIS 23 ~900 ka), the glacial-interglacial pulse became longer and more extreme. Early Middle Pleistocene interglacial high sea levels may have been the first to isolate hominin groups across ISEA, especially in the Arc. The Solo, Soa, and Cagayan basins show major faunal turnovers during MIS 23-20. EPR also marks the last fossil evidence of Early Pleistocene *Homo erectus* as defined at Trinil and Sangiran. With the Mid-Brunhes Event (MIS 11 ~450 ka), regional karst systems began to develop. By MIS 9 (~300 ka), caves were accumulating early hominin living debris and becoming an important record of fossil and archeological evidence. By the Last Interglacial (MIS 5e ~125 ka), ISEA early hominin groups were apparently isolated in at least three areas. Two lines of evidence illuminate some details of Middle and Late Pleistocene isolation.

Stegodontidae. The extinct family Stegodontidae comprised Asian relatives of mammoths and modern elephants. The fossil diversity of stegodon species is greatest near Yunnan, in southern China, their presumed area of origin. Pliocene

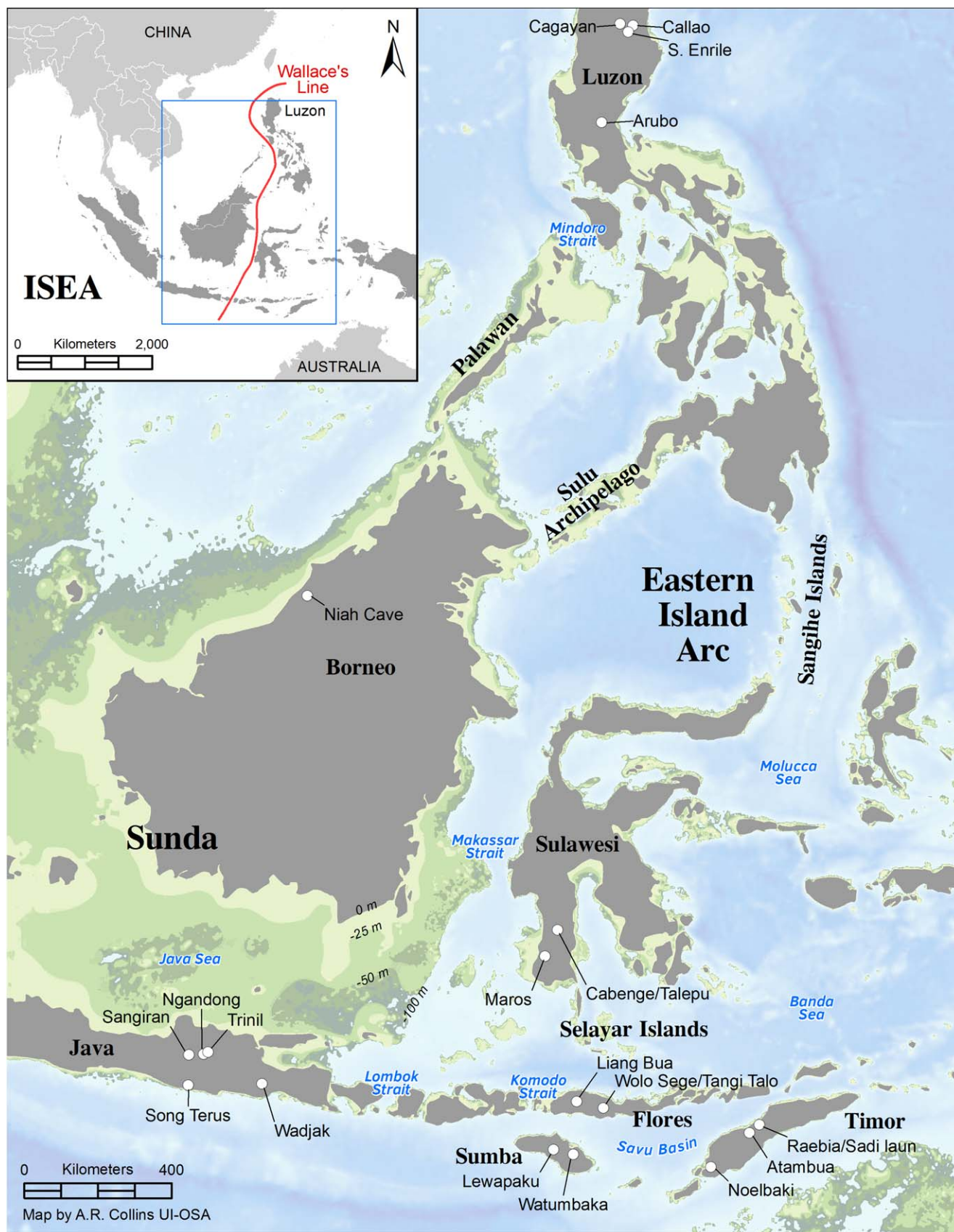


Figure 8. ISEA early hominin sites in bathymetric and geographic context including all geographic and a site names used in this paper. We followed Huxley's modification of Wallace's Line²⁰⁸ as illustrated in Cooper and Stringer²⁰⁴. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

TABLE 6. Pleistocene ISEA Stegodon-Artifact Co-occurrence Chart

Region	Island	Site	Geological context	Technology	Taxon	Age	Reference
Sunda	Java	Bukuran	Sangiran Fm	shell	<i>S. elephantoides</i>	1.6 Ma	19,32
Arc ^a	Flores	T. Talo+W. Sege	Ola Bula Fm	flake	<i>S. sondaari</i>	1.3 Ma	48
Arc	Sulawesi	Cabenge	Walanae Basin	flake	<i>S. sompoensis</i>	Early Pleist	48
Arc	Luzon	numerous	Cagayan Basin	LFA	<i>S. luzonensis</i>	0.8 Ma	96
Arc	Luzon	numerous	Arubo Basin	LFA	<i>S. luzonensis</i>	0.8 Ma	96
Arc	Timor	Atambua	Weaiwa Fm	flake	<i>S. timorensis</i>	n/a	79,83
Arc	Timor	Motaoan	Weaiwa Fm	flake	<i>S. timorensis</i>	n/a	87

^aEastern Island Arc

fossils are found across southern China and Japan. Pleistocene fossils are known in North China, South-east Asia, and India.^{172,173} In Pleistocene ISEA, *Stegodon* became a dominant faunal element in large- and small-bodied forms.^{85,174,175}

Large-bodied *Stegodon trigonoccephalus* is first documented in the middle Sangiran Formation (c. 1.6 Ma) of Java.²⁷ Presumably from Sunda, and with the aid of sea-level lowstands, *Stegodon* dispersed throughout ISEA. Earlier Pleistocene dwarfs appeared on Flores (*S. sondaari*), Sulawesi (*S. sompoensis*), Timor (*S. timorensis*), Sumba (*S. sumbaensis*), and Mindanao (*S. mindanensis*).³² Later in the Pleistocene, on Flores, a medium-bodied *S. florensis* probably gave rise to the Late Pleistocene small-bodied *S. florensis insularis*. The latter is known from the upper levels of Liang Bua, where dwarf hominins may have hunted or scavenged this and other dwarfed forms.¹⁵⁵

Dwarfing among ISEA Stegodontidae began during the earlier Pleistocene and continued throughout the epoch.³² The great preponderance of dwarfed forms is found east of Wallace's Line. Here, stegodon size reduction may be related to the increasingly high interglacial highstands commencing with the EPR. Body size reduction may in part explain the long-term success of select large mammals, including stegodon and hominins in the Arc.¹⁷⁶ West of Wallace's Line, on Sunda, there is no evidence of size reduction among hominins. Between the EPR (MIS 23 ~900 ka) and the Last Interglacial (MIS 5e ~125 ka), the Java hominins, as indicated by cranial and dental fossils at Sambungma-

can-Ngawi and Trinil (if later), did not decrease in size, nor is there indication of endemic dwarfing in Sunda stegodon.

There are several associations of stegodon fossils with early hominin artifacts, especially east of Wallace's Line. Minimally, such co-occurrences suggest that on the smaller Arc landmasses, early hominins and stegodontids frequented similar habitats. Maximally, as may be the case at Liang Bua, the association indicates that early hominins scavenged or hunted these proboscideans. Loosely speaking, the stegodon-artifact co-occurrence sequence appears to reflect early hominin dispersal across ISEA. The dispersal and isolation of Pleistocene ISEA stegodon may therefore serve as a heuristic model for insular development among ISEA early hominins. Table 6 summarizes this evidence.

With EPR (MIS 24-22, ~1.0-0.9 Ma), glacial period sea-level lowstands and aridity became more extreme. For large mammals, including hominins and stegodon, aridity may have prompted dispersal while sea-level lowstands enabled it. EPR thus provided the first real means to leave Sunda for the Arc and to set up Arc islands up first as glacial period refugia, then as interglacial period bottlenecks. A similar EPR forcing effect, to provide for early hominins and elephants (*Elephas* and *Mammuthus*) dispersing in tandem, has been suggested for southern Europe.^{60,61,177}

Homo floresiensis insularity. Among the larger vertebrates, small-bodied species have relatively more success in overwater dispersal and better survival potential on resource-limited islands.¹⁷⁰ With its small, specialized

morphology, the LB1 skeleton seems to show signs of insular evolutionary development. We can imagine that *Homo floresiensis* is the insular result of overwater dispersal of either of two forms, a small-bodied arrival that became further specialized or a larger-bodied arrival that became dwarfed.

At discovery, LB1's remarkably small brain size (417 cc) caused some researchers to argue that LB1 was a microcephalic modern human¹⁷⁸ or a pygmoid Australomelanesian modern human with developmental abnormalities¹⁷⁹ (Box 6). There is now convincing evidence that LB1 followed an insular evolutionary path for reduced brain size demonstrated in other mammalian lines. Three recent studies bear directly on *Homo floresiensis* brain size: island-dwarfed hippos; foxes, mice, and humans; and callitrichids (marmosets and tamarins). Weston and Lister¹⁸⁰ compared scaling models for dwarfed hippos and their mainland ancestors. Dwarfed species have significantly smaller brains, in relation to cranial size, than predicted from scaling mainland forms. Observing brain size reduction in multiple mammalian lines, Schaubert and Falk¹⁸¹ concluded that the *Homo floresiensis* brain could be proportionally dwarfed from a larger-bodied ancestor having similar relative brain size. Montgomery and Mundy¹⁸² correlated callitrichid brain size reduction with a slowdown of the prenatal growth rate. Based on the callitrichid example, the brain size of *Homo floresiensis* may have been subject to selection pressure at early stages of development.

The LB1 wrist has been compared with that of *Homo habilis*, known exclusively from East Africa (Box 6).

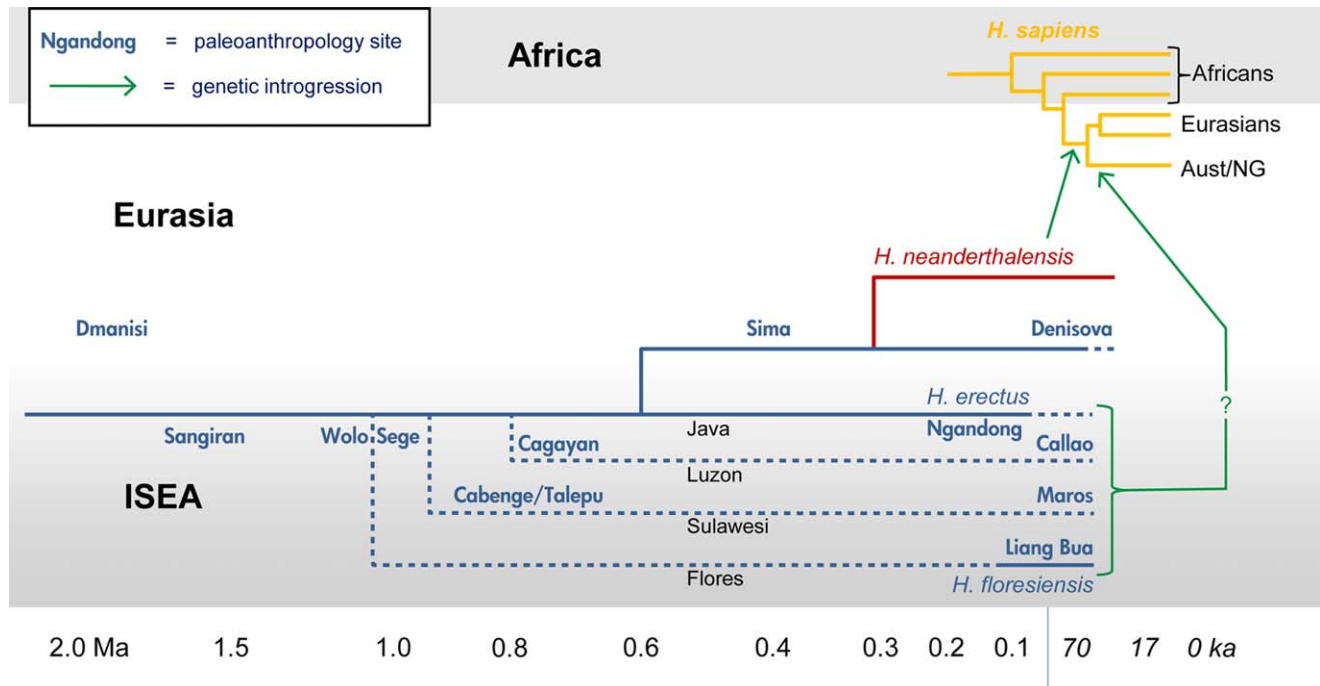


Figure 9. Hypothetical ISEA hominin lineages based on fossil, paleogenomic, and archeological evidence: yellow = *Homo sapiens*; red = *Homo neanderthalensis*; blue = *Homo erectus* and derived lines. On the *Homo erectus* line, archeological evidence provides divergence ages for Flores, Sulawesi, and Luzon early hominin lineages, presumably from Java origins. Green arrows show genomic introgressions to dispersing *Homo sapiens* from Eurasian Neandertals and, possibly, from ISEA *Homo erectus*-derived lines. Since *Homo heidelbergensis* is considered a descendant of *Homo erectus*, we assume that the paleogenomic evidence carried by *Homo erectus* is similar to that recorded recently at Sima de los Huesos in Spain.¹⁹⁸ (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

Late Pliocene or earliest Pleistocene ISEA dispersal of a small African hominin has thus been suggested.¹⁸³ Two lines of evidence weaken the Africa connection. First, LB1 has advanced craniodental features not seen in any African early hominin.^{184,185} Second, there is no fossil evidence across mainland Eurasia for a *Homo habilis* dispersal out of Africa.

Alternatively, *Homo floresiensis* represents a diminutive Eurasian arrival. Here, the Dmanisi fossils (Republic of Georgia, southwest Eurasia) reflect an Early Pleistocene (1.8 Ma) paleodeme¹⁸⁶ as a potential ISEA donor. Dmanisi *Homo erectus* features include a small brain (546–780 cc capacity) and small body (145–166 cm height, 40–50 kg weight).³ LB1 cranial capacity (417 cc) is not significantly smaller than that of Dmanisi skull 5 (D4500) (546 cc). A small-bodied representative of the Dmanisi paleodeme could have dispersed eastward across Wallace's Line at 1.3–1.0 Ma. Once on Flores, its wrist and foot specialized to local

conditions. If a larger-bodied Dmanisi hominin arrived at Flores in the same time frame, island dwarfing is implicated. In island contexts, ungulates can develop significantly shortened limb bones, shortened metapodials, and stiffer joints, sometimes resulting in fused elements.¹⁸⁷ Moreover, small-bodied hominins (*Australopithecus* and *Homo*) tend to have short, ape-like lower limbs as a function of body size scaling.¹⁸⁸

Currently, we conclude that LB1 can best be seen as the product of insular effects on a representative of the Dmanisi paleodeme. Likely pathways include the specialization of small-bodied arrival or the dwarfing of a larger-bodied arrival. Either way, LB1's small and specialized skeletal morphology reflects three features of Pleistocene Flores fauna: phylogenetic continuity, low species richness, and disharmony. "All three aspects stem from the isolated position of the island and have resulted in the distinct morphological characteristics of the Flores fauna."⁶

Modern Humans

The arrival date for *Homo sapiens* at ISEA and Sahul (New Guinea and Australia) is coalescing on a threshold of 47 ka.¹⁸⁹ ISEA's two well-dated early *Homo sapiens* sites fall on or near the threshold: ~47 ka at the Tabon Caves (Palawan, Philippines)⁹⁷ and ~42 ka at Niah Cave (Borneo, Indonesia).¹⁹⁰ Alternatively, Wadjak (Java, Indonesia), once considered the earliest ISEA modern human, has been radiometrically dated to 37–28 ka.¹⁹¹ Regarding Sahul, a much larger area with many more archeological sites, age determinations fall into a 47–40-ka interval.¹⁸⁹ The 47-ka arrival threshold suggests dispersal out of Africa toward the onset of MIS 3 (~59 ka), when renewed warmth and wetness made the normally arid areas of northwest Africa and Arabia more habitable than during the preceding MIS 4.^{192,193} Such conditions may have initiated the primary *H. sapiens* out-of-Africa dispersal.^{194–196}

At present, the latest ISEA early hominin fossil occurrences predate the 47 ka *H. sapiens* arrival threshold: Ngandong *Homo erectus* at ~143-130 ka,^{140,141,189} Liang Bua *Homo floresiensis* at ~60 ka,⁵⁰ and the Callao hominin at 66.7 ka.⁸ In sum, current evidence does not suggest significant overlap between early and modern hominins.

Denisovan Paleogenomics. Paleogenomics provides an emerging line of evidence for understanding the relationship between ISEA early and modern hominins during the Late Pleistocene (Fig. 9). Denisovan alleles have been identified in widely situated Eurasian Pleistocene contexts: extreme southwest and relatively early (Sima de los Huesos, 430 ka) and far northeast and much later (Denisova, 60 ka).¹⁹⁷⁻¹⁹⁹ The Sima mitochondrial sequence is identified as Denisovan and is distinct from that of Neanderthals.^{197,199} The Denisovan mtDNA genome shares, for at least one million years, a last common ancestor with the clade leading to *Homo sapiens* and Neanderthals.¹⁹⁷ The nuclear sequence shows a closer relationship to Neanderthals.²⁰⁰ The Denisovan genome is thus associated with several Eurasian early hominin lineages.²⁰¹ The genome also shows evidence of another, even older hominin lineage.^{197,202}

In modern human populations, Denisovan alleles appear in two widely spaced areas of Eurasia: Tibet²⁰³ and east of Wallace's Line, specifically in the Philippines and Sahul islands of New Guinea and Australia, and in Oceania.^{204,205} Given this far eastern distribution, Cooper and Stringer argue that Denisovan alleles introgressed into *Homo sapiens* populations east of Wallace's Line.²⁰⁴ Cooper and Stringer propose *Homo heidelbergensis* as the east-dispersing Denisovan-carrying early hominin. However, with no fossil evidence for this taxon in ISEA, the issue remains open. The ISEA Late Pleistocene early hominin fossil candidates for the introgression are Ngandong *Homo erectus*, *Homo floresiensis*, and the Luzon hominin, but it is not yet known if any of these species carried Denisovan alleles.

CONCLUSION

Among all Old World paleoanthropological areas, ISEA is unique in its great range of maritime environments. Pleistocene glacial eustasy gave the region a fast-changing character during the early hominin period. The current geography represents an extreme sea-level highstand with near maximum marine cover and terrestrial isolation. Such highstands typified relatively short periods of the Pleistocene. The generally longer glacial lowstands, ranging from ~20 m to ~125 m below present sea level, produced more continuous terrestrial exposures and the means for mammalian dispersal. Nevertheless, highstands were critical for isolating large mammalian fauna, including early hominins.

The spatial context for ISEA early hominin biogeography centers on Wallace's Line. For more than two million years, glacial eustasy, tectonic uplift, and volcanoclastic deposition have structured and restructured dispersal routes and province habitats east and west of the line. On Sunda, fossil evidence suggests that early *Homo erectus* arrived from mainland Eurasia during a low sea-level stand before 1.6 Ma (Solo Basin, Sangiran Formation). On the Arc, stone tools indicate that hominins arrived at the Soa (Flores) and Walanae (South Sulawesi) basins well before 1.0 Ma and to the Cagayan and Arubo basins (Luzon) probably by 800 ka.

The evidence of interglacial isolation is more subtle. By 300 ka, Sunda groups inhabited caves and used flake tools to process rhinoceros, tapir, and cervids (Gunung Sewu karst). Liang Bua cave opened for hominin habitation by ~195 ka, when the Flores hominin used an advanced flake tool industry in pursuit of the islands' endemic large fauna (Wae Racang karst). Most of the later evidence postdates the Last Interglacial (MIS 5e). By this time, morphological specializations include the large-brained Ngandong *Homo erectus* and the small *Homo floresiensis* body size and brain, both of which suggest that selection for these features developed before MIS 5e.

Liang Bua skeletal morphology likely represents development in relation to low rates of resource availability and predator stress. The diversification and dwarfing of ISEA Stegodontidae provides a relevant large mammalian fossil analogue. Liang Bua archeology indicates social and technological organization within which a very small human could consume large vertebrates. Parallels may be drawn with Late Pleistocene western Eurasia, where *Homo neanderthalensis* showed specializations in skeletal morphology and stone technology. The Last Interglacial may have isolated ISEA early hominin and stegodon populations to their evolutionary limits. The early hominin period apparently ended with the arrival of *Homo sapiens*.

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