Skeletal remains of a Pleistocene modern human (*Homo sapiens*) from Sulawesi

Adam Brumm1,*, David Bulbeck2, Budianto Hakim3, Basran Burhan4, Adhi Agus Oktaviana1,4, Iwan Sumantri6, Jian-xin Zhao7, Maxime Aubert1,5, Ratno Sardi3, David McGahan1, Andi Muhammad Saiful3, Shinatria Adhityatama4, Yousuke Kaifu8

1 Australian Research Centre for Human Evolution, Griffith University, Brisbane, Australia, 2 Archaeology and Natural History, School of Culture, History and Language, College of Asia and the Pacific, Australian National University, Canberra, Australia, 3 Balai Arkeologi Sulawesi Selatan, Makassar, Indonesia, 4 Pusat Penelitian Arkeologi Nasional (ARKENAS), Jakarta, Indonesia, 5 Place, Evolution and Rock Art Heritage Unit, Griffith Centre for Social and Cultural Research, Griffith University, Gold Coast, Australia, 6 Archaeology Laboratory, Hasanuddin University, Makassar, Indonesia, 7 School of Earth & Environmental Sciences, University of Queensland, St. Lucia, Queensland, Australia, 8 The University Museum, The University of Tokyo, Bunkyo, Tokyo, Japan

* a.brumm@griffith.edu.au

Abstract

Major gaps remain in our knowledge of the early history of *Homo sapiens* in Wallacea. By 70–60 thousand years ago (ka), modern humans appear to have entered this distinct biogeographical zone between continental Asia and Australia. Despite this, there are relatively few Late Pleistocene sites attributed to our species in Wallacea. *H. sapiens* fossil remains are also rare. Previously, only one island in Wallacea (Alor in the southeastern part of the archipelago) had yielded skeletal evidence for pre-Holocene modern humans. Here we report on the first Pleistocene human skeletal remains from the largest Wallacean island, Sulawesi. The recovered elements consist of a nearly complete palate and frontal process of a modern human right maxilla excavated from Leang Bulu Bettue in the southwestern peninsula of the island. Dated by several different methods to between 25 and 16 ka, the maxilla belongs to an elderly individual of unknown age and sex, with small teeth (only M1 to M3 are extant) that exhibit severe occlusal wear and related dental pathologies. The dental wear pattern is unusual. This fragmentary specimen, though largely undiagnostic with regards to morphological affinity, provides the only direct insight we currently have from the fossil record into the identity of the Late Pleistocene people of Sulawesi.

Introduction

The skeletal remains of anatomically modern humans (AMH) are rare in the Late Pleistocene record of Island Southeast Asia. The evidence at hand is currently limited to a small number of specimens excavated from Borneo, Java, Palawan, and Alor [1,2]. AMH remains are especially scarce in the Wallacean archipelago, or Wallacea [2], a biogeographically distinct zone comprised of thousands of oceanic islands (Fig 1). Wallacea lies between the edge of the Southeast Asian continental shelf (Sunda) and the ‘super-continent’ of Sahul, the landmass that emerged...
during the Pleistocene at times when global sea levels receded far enough to drain the shallow sea strait dividing mainland Australia from New Guinea. None of the ~2000 islands in Wallacea have ever been connected to Sunda or Sahul, even at the height of the Last Glacial Maximum (LGM; 22–19 ka) when global sea levels reduced by up to 130 m.

Wallacea has a long and enigmatic history of occupation by AMH. Current evidence suggests that the initial peopling of northern Sahul had taken place by 50 ka, as revealed by excavations at multiple localities across this region [3], and possibly by 70–60 ka, which findings at a single site (Madjedbebe) may indicate [4]. The latter claim remains contentious, however [3]. It has long been plainly evident that the first AMH group(s) to make landfall on Sahul must have colonised at least some parts of Wallacea first. At present, however, it remains uncertain which particular islands were settled by AMH during their earliest movements east of Sunda and which, if any, were left uncolonised. Theoretical debates continue over the precise marine voyaging route(s) used by AMH on their crossing from Sunda to Sahul, with the most widely investigated scenarios revolving around the northern route from Borneo via Sulawesi to the Bird’s Head of New Guinea and the southern route from Bali to Timor and thereafter to Australia [5–9]. However, it is now evident that both routes are theoretically possible. The current level of uncertainty surrounding the earliest movements of our species in the region largely stems from the lack of sustained research efforts in Wallacea [10,11]. Fieldwork projects focused on the Late Pleistocene period in the region have been increasing in number, scale, and scope over the past 20 years or so, but there are still relatively few well-dated sites from this key phase in the deep human past of Wallacea [10]. Presently, the oldest excavated
artefacts attributed to AMH date to around 44.6 thousand calibrated radiocarbon years before present (cal ka BP) at Laili cave in the eastern part of Timor (Timor-Leste) [12], while the earliest proxy evidence for our species comprises a figurative rock painting of an animal dated to at least 45.5 ka at the limestone cave of Leang Tedongnge in southern Sulawesi (see below) [13]. There is therefore a gap of several millennia between the oldest widely accepted sites in Sahul (~50 ka; [3]) and the earliest archaeological evidence attributed to our species in Wallacea.

The modern human skeletal record in Wallacea is particularly meagre [2]. Formerly, the oldest AMH skeletal remains consisted of three relatively complete individuals dating to ~17–12 ka at Tron Bon Lei rock-shelter on the small island (2100 km$^2$) of Alor in southeastern Wallacea [2,11] (Fig 1). Alor is adjacent to Timor and may have been one of the ‘last stops’ on the southern route to Sahul. It also lies on the eastern side of a major east-west division in the genetic diversity of modern people in Wallacea, the so-called ‘Malayan-Papuan Line’ (Fig 1) which separates the archipelago into two distinct genetic zones along a boundary running between Flores and Sumbawa in the south and the Malukus in the north [14]. On the western side, Y chromosome and mtDNA haplogroups are East Asian in origin, whereas to the east most people have an ancestral composition dominated by Papuan lineages. This abrupt transition in the genetic ancestry of people living on opposite sides of Wallacea reflects the ‘Neolithic’ settlement history of Austronesian-speaking farming societies from mainland Asia, but may also be partly explained by a much earlier and still poorly understood pattern of Late Pleistocene human migrations, including extensive LGM population movements [14]. Unravelling the origins of the Malayan-Papuan Line requires a far more complete record of Pleistocene *H. sapiens* fossils from both sides of this major east-west division in present-day peoples of Wallacea.

A confounding factor is the presence of two now-extinct hominin lineages (and possibly more) in Wallacea at around the time our species is thought to have established itself in the region: *Homo floresiensis* from the Late Pleistocene of Flores (~100–60 ka) [15–17], and *Homo luzonensis* from Callao Cave in the northern Philippines island of Luzon (~67 ka) [18]. In Sulawesi, the earliest archaeological evidence comes from the Walanae Depression in the island’s southwestern peninsula. These findings consist of stone tools excavated from deeply stratified deposits at an open-air site (Talepu) dated to ~194–118 ka [19]. The Talepu stone artefacts are technologically straightforward and are not associated with human fossils (as-yet undiscovered at this site). The identity of the hominins responsible for making them is not known [19]. It has also been hypothesised, based on complex statistical analyses of modern genetic data, that the Denisovans were split into at least two distinct lineages [20], one of which may have been present in Wallacea long before the first AMH arrived [21]. Indeed, it has even been proposed that one of these Denisovan branches reached Sahul (New Guinea) and persisted in this northern part of the continent until as recently as 30–14.5 ka [22]. This idea is contentious; if correct, it would imply that: 1) Denisovans inhabited Sahul at the same time as *H. sapiens*, apparently for a significant length of time; and 2) Denisovans were capable of major sea-crossings east of Sunda and thus potentially could have had an extensive geographical spread in Wallacea. Finally, the presence in the region of at least two other early human ‘ghost’ species is also inferred from patterns of archaic introgression in the genomes of modern-day people in various parts of Island Southeast Asia, Melanesia, and the wider region [23–25].

Given the empirical observations gleaned from the fossil record, and the various speculative hypotheses based on genetic data from humans both living and ancient, determining which lithic assemblages and other archaeological materials in Late Pleistocene Wallacea can be attributed to AMH, in the absence of their fossils, is not straightforward. This is especially so for Wallacean islands known or suspected to have been inhabited by archaic hominins close to the time of AMH colonisation.
Here, we report on the discovery of the first human skeletal remains from the Pleistocene of Sulawesi, the largest island in Wallacea and the most significant landmass on the northern route to Sahul and the western side of the Malayan-Papuan Line. Research into the prehistoric archaeology of Sulawesi began in the early twentieth century [26]; in fact, up until recent decades it was the most intensively explored island from an archaeological perspective in Wallacea, and, outside Java, in all of Indonesia. As with most parts of the region, however, research progress in Sulawesi has been slow and sporadic. Indeed, until well into the twenty-first century there had essentially been only two excavated archaeological localities that had produced dated evidence for Late Pleistocene human occupation [27,28]—two sites for an island which, at around 174,000 km$^2$, is the world’s eleventh largest. In this paper, we report on our ongoing excavations at the limestone cave of Leang Bulu Bettue in the south of Sulawesi, work that has uncovered a partial AMH maxilla and associated skeletal elements in deposits dating to between around 25 and 16 ka. We describe the context and chronology of the newly uncovered human fossil remains and present a morphological description of these materials.

Find context
The site of Leang Bulu Bettue is located in the limestone tower karst region of Maros in the southwestern peninsula of Sulawesi (Fig 1). The ~450 km$^2$ lowland karsts of Maros and the adjoining Pangkajene (or Pangkep) karsts further north lie between 4˚7’ S and 5˚1’ S [29]. This extensive karstic landscape harbours hundreds of caves and rock-shelters containing archaeological evidence for prehistoric human habitation, including parietal artworks (rock art). Concerning the latter, Uranium-series (U-series) dating of a coralloid speleothem associated with a hand stencil at Leang Timpuseng in Maros-Pangkep produced a minimum age estimate of 40 ka [30]. It is also evident that early humans continued to produce hand stencils in the karst caves and shelters of Maros-Pangkep until ~27–23 ka, based on bracketing U-series ages obtained from speleothem layers ‘sandwiching’ hand stencil art [30]. Most recently, U-series dating in the lowland karst district of Maros-Pangkep yielded securely dated evidence for what seems to be the world’s earliest known figurative representation of the animal world [13]. This rock art panel portraying Sulawesi warty pigs (Sus celebensis) has a minimum age of 45.5 ka, based on U-series dating of an overlying coralloid speleothem [13]. Until recently, the earliest excavated archaeological findings in the Maros-Pangkep karsts dated to 35.6–34.5 cal ka BP, as revealed by Glover’s 1975 excavations at Leang Burung 2 rockshelter in the Leang-Leang valley [28]; but see [31] for a major revision of the archaeological sequence at this well-known prehistoric site. Some 20 km to the north, in the Pangkep district, excavations at the high-level cave of Leang Sakapao 1 have yielded in situ stone artefacts and shellfish remains with a maximum age of 30–20 cal ka BP [27].

Elsewhere, we have published preliminary observations on the archaeological sequence at Leang Bulu Bettue, a new Late Pleistocene human occupation site in the Maros-Pangkep karsts [10,32,33]. Located in the Leang-Leang valley, Leang Bulu Bettue is a limestone cave and rockshelter positioned at valley-floor level around 20 km from the present shoreline to the west. It has a cave mouth measuring 4 m in width and 3 m in height, and an interior chamber that is 27.3 m long, 12.6 m wide, and up to 9.2 m high. The rockshelter area outside the cave extends for a distance of ~30 m along the base of the overhanging limestone cliff face. The shelter roof is located 15.6 m above the floor. Rock art at the site comprises undated red hand stencils (N = 37), most of which are poorly preserved. Superimposed on these traces of Pleistocene-style rock art are stylistically distinct charcoal drawings (including images of ‘dancing’ anthropomorphic figures) produced during the late Holocene [30].
Leang Bulu Bettue has been the focus of an annual program of joint Indonesian-Australian excavations carried out between 2013–15 and 2017–19. This work has uncovered a long sequence of stratified archaeological deposits inside the cave mouth and in the adjoining shelter (Fig 2). We excavated the deposit by stratigraphic layer using arbitrary 10 cm-deep spits, with in situ archaeological findings (e.g., stone artefacts, bones) measuring >10 mm in maximum dimension 3D-plotted using a total station. We wet-sieved cultural sediments on-site using 3 mm and 1 mm screens.

A number of findings from these excavations are reported elsewhere [10; see also 32,33]. Here we briefly describe the stratigraphic sequence and cultural remains pertaining to the uppermost Late Pleistocene deposits (Layers 1–5), relevant to the present study. We have partitioned this undisturbed sequence of sedimentary layers (Fig 3) into two discrete human occupation phases: Phase II: Historical (<1790 A.D.) and 'Neolithic' (1.7–1.6 ka cal BP); and Phase...
Fig 3. Stratigraphy and archaeological findings at Leang Bulu Bettue (2017). Top: East wall profile of the 2017 rock-shelter excavations, showing the stratigraphic sequence (note: Layers 4c-f are not visible here). Bottom: Spatial distribution of stone artefacts, faunal remains, and other findings recovered during the 2015–17 excavations, color-coded by stratigraphic layer (prepared using ArcScene). The location of the modern human right maxilla (Maros-LBB-1a) in relation to Stalagmite 437 is indicated by a white star.

https://doi.org/10.1371/journal.pone.0257273.g003
I: MIS 3/2 (~50–16 ka). The Late Pleistocene cultural deposits of Phase I consist of silty clays with dense archaeological findings (Layers 4a–e). These sedimentary units are up to 1.5 m thick and span ~29.5–16 ka. Below this sequence is Layer 4f, a 50 cm-thick sandy clay layer dated to around 40–30 ka. Below Layer 4f is Layer 5, a 50 cm-thick sandy clay with relatively few cultural remains and faunal materials. Layer 5 has an estimated age of 50–40 ka.

The Late Pleistocene human skeletal remains described in this paper were excavated in situ during the 2017 field season. They were recovered from the upper part of the stratified and undisturbed Layer 4a (Fig 3), a ~70 cm thick moderate yellowish brown (10YR5/4) slightly sandy ‘mud’ (silt = 50.3%, clay = 32.2%). No other human remains have been found in Layer 4a. The skeletal elements were recovered in close association amidst profuse remains of what we consider to be ‘domestic’ activities, including lithic debris from stone artefact production and fragments of burnt animal bones reflecting food preparation and consumption. We encountered no evidence for a burial in Layer 4a. We also observed no clearly associated features or findings that could reasonably be interpreted as indicative of special contexts for the disposal of the human remains. The recovery of these isolated skeletal materials could be suggestive of the presence of burials in as-yet unexcavated portions of Layer 4a at the site.

The richest cultural and faunal assemblages excavated at Leang Bulu Bettue are found in Layer 4a [10]. The lithic technology used by the Layer 4a inhabitants was focused on chert reduction. It involved two stone-flaking techniques—direct freehand hard-hammer percussion; and anvil-supported bipolar percussion, where the blank was supported on a hard surface and the top edge struck, initiating flakes from the struck edge and the anvil support [10]. The dense faunal assemblage is dominated by shells of freshwater gastropods, mostly *Tylomelania perfecta*. The most frequently represented mammal remains are those of the bear cuscus (*Ailurops ursinus*), and various rodents. Sulawesi warty pig (*S. celebensis*) is the largest animal represented in Layer 4a. These ~40–85 kg wild suids are endemic to Sulawesi, although there is some evidence to suggest the species was translocated to various other Wallacean islands (and possibly further afield) in late prehistory [34]. We also uncovered findings indicative of symbolic behaviour in Layer 4a, including a drilled pendant made from an *A. ursinus* phalanx and several engraved stone artefacts, some of which consist of flaked chert artefacts with geometric motifs incised into cortical surfaces [10]. Two stone ‘plaquettes’ engraved with what seem to be figurative motifs have also been recovered [33]. Evidence for pigment use in Layer 4a includes utilised mineral colorant nodules and ochre residues on the surfaces of both stone and bone tools [10].

**Antiquity of the human remains**

Prior dating work [10,32], and new evidence presented here, allows us to constrain the age of Layer 4a to between 24.8 and 16 ka, thus broadly within the timespan of the LGM. As far as we have been able to ascertain no charcoal is preserved in the Late Pleistocene deposits at Leang Bulu Bettue. Hence, the chronology for Layer 4a is based on four independent dating methods: 1) U-series isotope analysis undertaken on vertical, still-emplaced stalagmites exposed during excavations of Layer 4a/b; 2) AMS $^{14}$C-dating of *T. perfecta* shells recovered in situ from Layer 4a; 3) laser ablation U-series dating of a pig tooth excavated from Layer 4a; and 4) optical dating (post-infrared infrared stimulated luminescence [pIRIR]) of feldspars from Layer 4a.

**Stalagmite chronology.** We dated three speleothem samples associated with Layer 4a: Stalagmite 485 (Fig 4) and Stalagmite 437 (Fig 5), which both formed above this layer, and Stalagmite 605, which formed below it (Fig 4). The results of U-series dating of these three stalagmites are provided in Table 1. Following collection in the field, the stalagmites were sawn longitudinally. In the case of Stalagmites 485 and 605, trace element analyses were conducted...
along the growth axes to identify calcite layers with the greatest U-series dating potential. Trace element analysis was not undertaken on Stalagmite 437. U-series isotope analyses of the three stalagmites were carried out in the Radiogenic Isotope Facility of the University of Queensland, Brisbane, on a Nu Plasma multi-collector inductively coupled mass spectrometer (MC-ICP-MS), following chemical separation procedures and MC-ICP-MS analytical protocols described elsewhere [35,36]. The $^{230}$Th/$^{234}$U ages were calculated using Isoplot EX 3.75 [37] and half-lives of 75,690 years ($^{230}$Th) and 245,250 years ($^{234}$U) [38].

Stalagmite 485 (height: 35.6 cm, basal width: 15.7 cm) and Stalagmite 605 (height: 18 cm, diameter: ~11 cm) were exposed during the 2013 excavations. Initial U-series dating results for these speleothems are reported elsewhere [10] (Fig 4). The two stalagmites were uncovered during excavation of Square A1 inside the cave mouth ~500 cm north of the human skeletal...
| Stalagmite No | Sub-Sample | Sub-sampling depth (mm) | Wt (g) | 238U (ppm) | 232Th (ppb) | (230Th/232Th) ±2σ | (230Th/238U) ±2σ | 234U/238U ±2σ | Uncorrected Age (ka) ±2σ | Corrected Age (ka) ±2σ | Initial (234U/238U) ±2σ |
|--------------|------------|------------------------|-------|------------|-------------|---------------------|------------------|------------------|------------------------|------------------------|-----------------------|
| 485          | 0055       | 5.5                    | 0.04533 | 0.947      | 7.70        | 18.16 ± 0.11        | 0.0486           | 0.0003 | 0.5242 ± 0.0004 | 10.77 ± 0.07 | 10.29 ± 0.26 |
| 485          | 0435       | 43.5                   | 0.03640 | 0.786      | 9.30        | 13.17 ± 0.10        | 0.0513           | 0.0004 | 0.5278 ± 0.0007 | 11.32 ± 0.09 | 10.64 ± 0.37 |
| 485          | 0835       | 83.5                   | 0.04809 | 0.785      | 8.24        | 14.50 ± 0.15        | 0.0502           | 0.0005 | 0.5247 ± 0.0006 | 11.14 ± 0.12 | 10.52 ± 0.34 |
| 485          | 1375       | 137.5                  | 0.02775 | 0.753      | 22.6        | 6.11 ± 0.08         | 0.0605           | 0.0008 | 0.5287 ± 0.0008 | 13.480 ± 0.19 | 11.73 ± 0.95 |
| 485          | 1560       | 156                    | 0.02380 | 0.94       | 50.27       | 4.12 ± 0.04         | 0.0722           | 0.0007 | 0.5311 ± 0.0006 | 16.28 ± 0.17 | 13.1 ± 1.7 |
| 485          | 1850       | 185                    | 0.02406 | 0.920      | 50.64       | 4.11 ± 0.06         | 0.0744           | 0.0011 | 0.5265 ± 0.0009 | 17.01 ± 0.29 | 13.7 ± 1.8 |
| 437          | e          | 76                     | 0.00218 | 0.562      | 55.82       | 3.44 ± 0.07         | 0.1126           | 0.0023 | 0.6180 ± 0.0013 | 22.44 ± 0.52 | 17.4 ± 2.8 |
| 437          | d          | 96                     | 0.00363 | 0.622      | 44.94       | 4.66 ± 0.06         | 0.1110           | 0.0015 | 0.6300 ± 0.0013 | 21.58 ± 0.32 | 18.0 ± 2.0 |
| 437          | c          | 123                    | 0.00596 | 0.576      | 145.52      | 2.74 ± 0.03         | 0.2284           | 0.0029 | 0.6686 ± 0.0014 | 47.54 ± 0.79 | 34.9 ± 7.7 |
| 437          | b          | 127                    | 0.00581 | 0.576      | 274.07      | 2.37 ± 0.02         | 0.3724           | 0.0032 | 0.6660 ± 0.0016 | 99.6 ± 1.7 | 72 ± 2.2 |
| 437          | a          | 129                    | 0.00479 | 0.643      | 459.04      | 2.35 ± 0.02         | 0.5529           | 0.0035 | 0.6795 ± 0.0020 | unable to calculate | |
| 605          | 0274       | 27.4                   | 0.01997 | 1.334      | 3.78        | 111.42 ± 0.77       | 0.1039           | 0.0007 | 0.5284 ± 0.0010 | 24.73 ± 0.20 | 24.56 ± 0.23 |
| 605          | 0780       | 78                     | 0.01840 | 1.82       | 37.85       | 16.50 ± 0.08        | 0.1128           | 0.0005 | 0.5272 ± 0.0008 | 27.30 ± 0.16 | 26.04 ± 0.74 |
| 605          | 1230       | 123                    | 0.01792 | 1.47       | 4.53        | 102.07 ± 0.57       | 0.1038           | 0.0006 | 0.5257 ± 0.0008 | 24.86 ± 0.16 | 24.68 ± 0.19 |
| 605          | 1599       | 159.9                  | 0.01928 | 1.064      | 16.41       | 22.43 ± 0.20        | 0.1141           | 0.0010 | 0.5321 ± 0.0008 | 27.34 ± 0.28 | 26.41 ± 0.60 |
| 605          | 1900       | 190                    | 0.00775 | 1.340      | 26.01       | 17.86 ± 0.11        | 0.1142           | 0.0007 | 0.5380 ± 0.0012 | 27.01 ± 0.21 | 25.86 ± 0.69 |

This table contains the results of U-series disequilibrium dating of three stalagmites: Stalagmites 485, 437, and 605. Note: Ratios are activity ratios calculated from the atomic ratios. Errors are at 2σ level. The ages are calculated using Isoplot 3.75 Program [37] with decay constants from Cheng et al. [38]. Corrected ages were calculated assuming initial/detrital 230Th/232Th activity ratio equal 0.825 (± 50%) (the bulk-Earth value, which is the most commonly used for initial/detrital 230Th corrections). Sub-sampling depth denotes the depth at which each sample was collected from the tip of the stalagmite along the main growth axis.

https://doi.org/10.1371/journal.pone.0257273.t001
remains find spot. Both samples comprise in situ upright stalagmites. Stalagmite 485 is the stratigraphically youngest sample. This speleothem formed on the upper surface of Layer 4a. Stalagmite 605 grew on the upper surface of underlying Layer 4b. It was buried at a later stage by the accumulation of Layer 4a, suggesting there was a depositional hiatus between these layers. Both stalagmites formed on top of ~10–15 cm-thick pedestals of cemented sediment and archaeological detritus. Archaeological inclusions in the pedestals consist of shell, bone, ochre, and lithic artefacts. These pedestals appear to have formed as a result of calcium carbonate-enriched water dripping from the overhead ceiling and forming a hardened mass on the soft sedimentary deposits of the cave floor.

Stalagmite 437 is a vertical and still in situ stalagmite that formed atop the sloping upper surface of Layer 4a in the rock-shelter area (Fig 5). Stalagmite 437 is irregular in form. The speleothem portion is 8 cm in height and 10 cm in width, and 9.5 cm thick at the base. Below the basal growth layers was a pedestal of cemented archaeological deposit measuring 17 cm in depth by 15 cm in width by 14 cm in thickness and containing characteristic Layer 4a findings, such as T. perfecta shells and flaked chert artefacts. The human skeletal remains were recovered a distance of 38 cm to the south of Stalagmite 437 and 3.5 cm below the base of this intact speleothem.

As has been previously noted, Stalagmite 485 is located immediately above Layer 4a and thus the basal growth age of this speleothem provides us with a minimum age for this archaeological horizon. Six (n = 6) U-series ages estimates (sub-samples 0055, 0435, 0835, 1375, 1560, 1850) were calculated along the main growth axis of the speleothem (Fig 4, Table 1). Their $^{230}$Th/$^{232}$Th activity ratios range between 4.11 and 18.16. The cleanest samples (n = 3) are located towards the tip of the speleothem, with analytically indistinguishable ages of 10.3 ± 0.3 to 10.5 ± 0.4 ka. The other samples (n = 3) are located towards the base of the speleothem and their ages range between 11.7 ± 1.0 to 13.7 ± 1.8 ka. The oldest minimum age for Layer 4a is determined by sub-sample 1850, with a detrital-$^{230}$Th corrected age of 13.7 ± 1.8 ka. Layer 4a is therefore at least 11.9 ka and could be at least as old as 15.5 ka. This also corresponds to the base of the speleothem having formed immediately above Layer 4a.

Stalagmite 605 is located below Layer 4a and has formed immediately above Layer 4b. Five (n = 5) U-series ages estimates (0274, 0780, 1230, 1599, 1900) were calculated along the growth axis of the speleothem (Fig 4, Table 1). The sub-samples are all relatively clean, with $^{230}$Th/$^{232}$Th activity ratios ranging between 16.50 and 111.42. Their ages range between 24.6 ± 0.2 ka to 26.4 ± 0.6 ka. The youngest maximum aged for Layer 4a is determined by sub-sample 0274 with a detrital-$^{230}$Th corrected age of 24.6 ± 0.2 ka, suggesting the layer could be younger than this age. This also corresponds to the tip of the speleothem having formed before
the deposition of Layer 4a. Thus, based on the stratigraphical context of the above three stalagmites, we infer that Layer 4a can be securely bracketed into 18 ± 2 to 24.6 ± 0.2 ka.

**Radiocarbon dating.** We conducted AMS $^{14}$C dating on a $T.$ perfecta shell that was excavated in situ from near to the top of Layer 4a inside the cave (131 cm depth, Squares A1 and A2). This shell was located ~10 cm below the pedestal of cemented archaeological detritus underlying Stalagmite 485. It yielded an AMS $^{14}$C age (Wk-37742) of 18,126 ± 51 BP or 22.2–21.9 cal ka BP at 2σ. This date was calibrated in OxCal 4.4 using an unconstrained mix of the IntCal20 and SHCal20 revised calibration curves, as recommended in Hogg et al. 2020 [39]. With regards to this age estimate on $T.$ perfecta shell, it has not been possible thus far to calculate the magnitude of the freshwater reservoir (or hardwater effect) in Maros-Pangkep [27,31].

**Optical dating.** As reported elsewhere [32; see also 10], we conducted pIRIR-dating on Layer 4a feldspars (LBB-I) collected from the south wall of Square A2 at about 8 cm below the level of sample Wk-37742, yielding a depositional age of 21.4 ± 2.5 ka (68.2% probability [1σ]) for Layer 4a. Reported at the 95.4% confidence interval, error ranges for the pIRIR feldspar (16.4–26.4 ka) age suggest the upper part of Layer 4a is at least 16 ka, which, again, is consistent with the U-series ages obtained from the two in situ stalagmites that developed immediately on top of this layer (Stalagmites 485 and 437).

**U-series dating of fossil tooth.** We conducted laser ablation U-series dating on a suid molar recovered from Layer 4a (LBB3 1B-14B). The specimen was collected at a depth of 156 cm. Results indicate a minimum age of 15.9 ± 0.5 ka (1σ) for this tooth. This is also consistent with the stalagmite chronology, which indicates that Layer 4a dates to more than 16 ka.

**Summary of dating results for Layer 4a.** Previously, we inferred an age of 26–22 ka for Layer 4a based on four independent dating methods [10]. In that prior work, the $^{14}$C date for the freshwater shell (Wk-37742) from below Stalagmite 485 was used as a reasonable estimate for the upper age of Layer 4a (~22.3 cal ka BP). Based on the uncertainties introduced owing to the freshwater reservoir effect, however, we now prefer to rely on the U-series stalagmite chronology, including new dates reported for the first time here. This suggests an age of 24.8–16 ka for Layer 4a in which the human remains were recovered.

**Summary of the human remains**

The key specimen, designated Maros-LBB-1a, consists of a nearly complete palate and frontal process of the right maxilla (Figs 6 and S1). The former consists of several fragments (combined weight 18 grams) excavated in situ in Square -F1 (Spit 10), and the latter was recovered from wet-sieving of the same square and spit. An evident point of contact between the elements was discerned at the inferior nasal aperture, leading to the inference of a vertically short nasal aperture, and a reconstruction with plasticine inserted to simulate the missing maxillary bone.

The right maxilla contains the first to third right upper molars ($M^1$, $M^2$, and $M^3$). In addition, a left maxilla fragment weighing 1 gram was recovered from nearby Square E1 (Spit 11), and two conjoining mandible fragments (combined weight 3 grams) were also excavated from Square E1 (Spit 12) and Square G2 (Spit 11); however, these specimens are too fragmentary for analysis and hence they are not considered further here. All of these skeletal materials (including the undiagnostic elements) are considered to come from a single individual. The Maros-LBB-1a skeletal remains (and associated fragments) are unburnt and their partly mineralised condition is in keeping with the majority of Late Pleistocene faunal elements excavated so far from Layer 4a.

**Methods**

The Indonesian field research was authorised by Indonesia’s State Ministry of Research and Technology (RISTEK) and was conducted in collaboration with counterpart institution Pusat
Penelitian Arkeologi Nasional (ARKENAS), Jakarta, Indonesia. All necessary permits were obtained from Indonesia’s State Ministry of Research and Technology for the described study (Permit No: 154/SIP/FRP/E5/Dit.KI/VII/2017), which complied with all relevant regulations. The human skeletal remains from Leang Bulu Bettue (specimen number: Maros-LBB-1a) are permanently stored at the premises of the Balai Arkeologi Sulawesi Selatan (Makassar Archaeology Office in South Sulawesi) in Makassar, South Sulawesi. Requests to access collections for study, including databases and catalogs of finds, should be directed in the first instance to the directors of Pusat Penelitian Arkeologi Nasional (ARKENAS) (http://arkenas.kemdikbud.go.id/#1) and Balai Arkeologi Sulawesi Selatan (https://balar-sulsel.kemdikbud.go.id).

Morphological analysis

The methodology for the analysis of Maros-LBB-1a closely followed the techniques applied by DB to Gua Cha in Peninsular Malaysia [40] so as to assist comparison with this substantial assemblage of mid-Holocene burials from an Island Southeast Asian rainforest environment. The three *in situ* teeth were measured for their maximum mesio-distal and bucco-lingual diameters and also these diameters at the cemento-enamel junction. Cranial measurements followed the definitions in Bräuer [41] and Howells [42]. Measurements of Maros-LBB-1a...
were taken with a Kincrome electronic calliper accurate to 0.01 mm (generally rounded off to the closest tenth of a millimetre). Oral pathology was recorded following Patterson [43], although indications of periodontal disease are inferred here following Tayles [44:238]. Dental morphology features recorded were those of the Arizona State University (ASU) system [45] including reference to standard plaques illustrated in that work and Hillson [46] for photographs of Carabelli’s cusp development. Cranial morphology was recorded following Larnach and Macintosh [47].

Taxonomy

The Leang Bulu Bettue individual (Maros-LBB-1a) is clearly different from two representative pre-modern hominin groups in the region, *Homo erectus* from Java and *H. floresiensis* from Flores. The latter exhibits a distinctly protruded maxillary process of the malar, as reflected by an anteriorly positioned lateral nasal margin and laterally faced bone surface beside it, which is marked posteriorly by the formation of an infraorbital (maxillary) sulcus, modest alveolar
prognathism, a mesiodistally elongated $M^2$ crown, and a lingual molar root that diverges strongly medially [48–50]. Maros-LBB-1a displays enhanced alveolar prognathism and the relatively short $M^2$ crown is outside the range of variation for $H$. erectus (Fig 7). It is also divergent from $H$. floresiensis (Fig 7). Theoretically, Maros-LBB-1a could belong to a member of the now-extinct and apparently geographically widely dispersed hominin Denisovan branch, but no Denisovan cranial remains have been identified [51] to allow this possibility to be tested. Rather, as described below, Maros-LBB-1a clearly falls within the morphological range of $H$. sapiens in the region and so is assigned to AMH.

**Age and sex of Maros-LBB-1a**

This AMH individual is evidently adult, as shown by the worn status of the extant $M^3$ (Fig 6, Table 3). As reconstructed, the extant remains suggest an individual of small to medium size:

Table 2. Comparative *Homo sapiens* sample (see Fig 7).

| Region                      | Remarks                                                                 | N*  | Repositoryb |
|-----------------------------|-------------------------------------------------------------------------|-----|-------------|
| **Prehistoric Southeast Asia** |                                                                         |     |             |
| Flores'                     | Aimere, Gua Alo, Gua Nempong, Liang Bua, Liang Momer, Liang Toge, Liang X | 9   | NBC, ARKENAS |
| Java'                       | Hoekgrot, Wajak                                                           | 3   | NBC         |
| Malaysia'                   | Guar Kepah                                                               | 19  | NBC         |
| Vietnam'                    | Mai Da Dieu, Mai Da Nuoc, Hang Chim, Dong Cang, Con Co Ngua              | 73  | IAH         |
| **Australia/Melanesia**     |                                                                         |     |             |
| New Guinea'                 |                                                                         | 30  | AMNH, MH    |
| Australia/Tasmania Aboriginal Australian' |                                              | 19  | AMNH        |
| **Southeast Asia**          |                                                                         |     |             |
| Philippine ‘Negrito’        |                                                                         | 20  | MH          |
| Others                      | Andaman, Indonesia, Malaysia, Nicobar, Philippine, Singapore, Thailand  | 57  | AMNH, MH    |
| **Northeast Asia**          |                                                                         |     |             |
| Northeast Asia              | China, Chukuci, Korea, Mongol, Yukagir                                    | 18  | AMNH        |
| **Africa**                  |                                                                         |     |             |
| ‘Bushman’                   |                                                                         | 17  | AMNH, MH    |
| African ‘Pygmy’             |                                                                         | 20  | MH          |
| South Africa                | Excluding ‘Bushman’                                                       | 26  | AMNH        |
| East Africa                 |                                                                         | 45  | AMNH        |
| West Africa                 | Excluding ‘Pygmy’                                                        | 55  | AMNH        |
| **Indo/Europe**             |                                                                         |     |             |
| India                       |                                                                         | 6   | AMNH        |
| German                      |                                                                         | 65  | AMNH        |
| Others                      | Hungary, Poland, Sweden                                                  | 8   | AMNH        |
| Total                       |                                                                         | 490 |             |

*Samples included in the EFAs.
*Number of individuals.

https://doi.org/10.1371/journal.pone.0257273.t002
• estimated (right) nasal height of ~42 mm, similar to the averages recorded for Andaman Islander females and Khoisan males and females, but smaller than the averages recorded by Howells [42] for any other male or female series;

• estimated nasal breadth (based on doubling the extant right breadth) of 27 mm, which is similar to the averages recorded for Southwest Pacific females, and Polynesian/Micronesia, Ainu and Khoisan males and females [42].

The palate is of medium size [52] with its length and estimated breadth of respectively 60 and 64 mm producing a module of 38.4. The teeth are quite small in size, with available measurements that either fall reasonably close to the averages for 2nd millennium CE burials from Southeast Sulawesi or below their recorded range (Table 4). However, the particularly small Maros-LBB-1a tooth diameters reflect loss of the bulkiest part of the crown due to advanced occlusal attrition (Fig 6, Table 3) and so we focus on the tooth diameters at the cemento-enamel junction. Doing this, and including comparative data from the (sexually and chronologically, comprehensively overlapping) Gua Cha teeth in Peninsular Malaysia, we see that the Maros-LBB-1a tooth diameters fall within the lower median of the comparative range (Fig 8).

In summary, sex is difficult to estimate for such fragmentary remains, especially without knowing the specimen’s comparative population. It is noteworthy, however, that the Tron Bon Lei individuals are surprisingly small in size, being ‘unique even by Pleistocene standards in the combination of small and narrow morphologies’ [2: p12].

**Oral disease**

We infer that this Late Pleistocene individual experienced poor oral health (Fig 9). The absence of any teeth other than the molars could be due to their loss after death, although none of them were recovered during excavation. Certainly, the modestly resorbed P1 alveolus (Fig 9) indicates that this tooth had been lost prior to the individual’s death, and the advanced dehiscences and rough socket surfaces at the incisor and canine sites (Fig 9) also suggest that these teeth had lost their anchoring before death. In addition, interproximal inflammation [43] was moderate to extensive at all tooth sites anterior of the M2, and all of the tooth sites show evidence for what we interpret as the effects of periodontal disease (Table 5). A level of antemortem tooth loss possibly as high as 50% of preserved sockets seems relatively high compared with other Pleistocene human fossil assemblages (see, e.g., [55]). At Grotte des Pigeons in Morocco, some 29% of post-canine teeth lost before death is recorded amongst biologically ‘old’ AMH adults of terminal Pleistocene antiquity, a phenomenon attributed to heavy occlusal attrition and cariogenic carbohydrates of a diet based on fermented pine nuts and acorns [56]. In Maros-LBB-1a, the only observable caries are pinhole-sized cavities in the anterior and central

| Tooth          | Occlusal wear | Calculus location                                      | Calculus amount |
|----------------|---------------|--------------------------------------------------------|-----------------|
| First molar    | 4’            | Radicular: disto-buccally and disto-lingually           | Slight          |
| Second molar   | 3             | Coronal: mesio-buccally                                 | Slight          |
| Third molar    | 7             | Radicular: entire buccal and distal surfaces, and disto-lingually | Moderate       |

*The mesio-lingual corner of the tooth was chipped off during life, making assessment of the tooth’s occlusal wear problematic.

https://doi.org/10.1371/journal.pone.0257273.t003
foveae of the M\textsuperscript{2}. Hence, a closer comparison may be afforded by the Hoabinhian hunter-gatherer teeth from Gua Cha in the Peninsular Malaysia rainforests—a dramatic increase in dehiscences, interproximal inflammation and other periodontal disease with increased dental wear, but maintenance of a caries rate affecting only about 40% of teeth [40].

Maros-LBB-1a also exhibits a distinctive dental wear pattern (Figs 6 and 9). Only the M\textsuperscript{2}, the occlusal surface of which projects below the other two extant molars, has a normal occlusal plane. The wear plane of the first molar slopes strongly upward from the distal to the mesial margin. A possible explanation for this unusual condition is that the first premolar alveolar surface had atrophied to the point where almost the entire root socket had been lost. Accordingly, during eating, the food bolus was masticated in a pronounced upward direction anteriorly from the first molar to the first premolar. On the other hand, the wear plane on the M\textsuperscript{3} slopes strongly upward mesially to distally. This would appear to be not due to mastication but instead the extensive use of this tooth as a tool; for instance, dragging palm fronds up the molar surface to produce twine. Possible evidence for this suggested paramasticatory (nondietary) dental use comes from the presence of a thin but clear striation running from the mesiolingual to the bucco-distal surface of the tooth. Grooves on the anterior teeth resulting from twine production or similar activities are reported in the literature [57], but, in the case of Maros-LBB-1a, a striation rather than a groove is involved and the affected tooth is the most posterior in the dentition. Further assessment of the unusual tooth wear and oral pathology of the Leang Bulu Bettue palate is difficult for a damaged, isolated fragment.

### Table 4. Diameters (mm) of the Maros-LBB-1a molars, with Southeast Sulawesi comparisons (from [34]; Bulbeck laboratory observations).

| Tooth                    | Maros-LBB-1a | Gua Lampetia/Gua Andomo/Gua Sambangoala |
|--------------------------|--------------|-----------------------------------------|
|                          | Measurement  | Average (range)                         |
| First upper molar        | Mesio-distal diameter | > > 8.5\textsuperscript{*} | 10.4 (9.6–11.4) |
| Second upper molar       | ''            | 9.8                                    | 9.7 (9.0–10.7) |
| Third upper molar        | ''            | 9.2\textsuperscript{*}                | 9.8 (9.5–10.0) |
| First upper molar        | Bucco-lingual diameter | 12.2 | 11.7 (10.6–12.6) |
| Second upper molar       | ''            | 11.6                                   | 11.6 (10.9–13.4) |
| Third upper molar        | ''            | 10.7\textsuperscript{*}               | 11.5 (11.0–12.4) |
| First upper molar        | Mesio-distal diameter at cemento-enamel junction | 8.1 | 8.6 (8.0–9.5) |
| Second upper molar       | ''            | 7.9                                    | 8.3 (7.0–9.6) |
| Third upper molar        | ''            | 7.0                                    | 9.0 (8.9–9.1) |
| First upper molar        | Bucco-lingual diameter at cemento-enamel junction | 11.9 | 11.3 (10.3–12.4) |
| Second upper molar       | ''            | 11.5                                   | 11.0 (10.0–13.0) |
| Third upper molar        | ''            | 11.1                                   | 11.3 (10.8–12.2) |

\textsuperscript{*}Cannot be measured with any reliability due to advanced interproximal wear.
\textsuperscript{*}Somewhat reduced from advanced occlusal wear.

https://doi.org/10.1371/journal.pone.0257273.t004
Teeth—Other observations

No signs of macroscopic enamel linear hypoplasia were observed on any of the extant molars of Maros-LBB-1a.

Observations on the root and crown morphology of Maros-LBB-1a are compatible with either a Sunda-Pacific (Southeast Asian/Micronesian/Polynesian) or a Sahul-Pacific (Australo-Melanesian) affinity, based on comparisons with the data in Scott and Turner [45]. The two-rooted first upper premolar (Fig 6) characterises ~40–60% of Sunda-Pacific and ~30–45% of
Sahul-Pacific populations. The three-rooted upper second molar is found with ~50–80% of Sunda-Pacific and ~55–80% of Sahul-Pacific populations. The absence of enamel extension on the first upper molar (or any of the Maros-LBB-1a molars) characterises more than 80% of Sahul-Pacific populations and Micronesians, and is otherwise observed on ~65–80% of other Sunda-Pacific populations. Based on hypocone development recorded as ASU grade 4, the second upper molar can be clearly classified as four-cusped, as also recorded for 85–92% of Sunda-Pacific populations and consistently >90% of Sahul-Pacific populations.

Similarly, statistical analysis of dental morphology shows that the four closest populations to Gua Cha [58] are Sunda-Pacific (Polynesia, 'Early Southeast Asia') or Sahul-Pacific (Aboriginal Australia, Melanesia).

Cranial morphology

The anterior nasal spine is absent (Broca 1), and the right lower narial margin is represented by a thin line dividing the nasal and alveolar planes (non-anthropine of Larnach and Macintosh [47]). The lateral orbital margin of the malar is not preserved, but the medial (maxillary) section of the orbit appears to be trending towards a rounded orbital border. Medial to the orbit, the superior surface of the frontal process faces anterolaterally, suggesting at least modest anterior protrusion of the nasal bridge. Although the exact orientation in the original facial skeleton is unknown for the isolated frontal process, viewed laterally, the nasofrontal suture slopes anteriorly while the nasal margin follows a more vertical orientation. The surface immediately lateral to the lateral nasal margin forms a posteriorly ‘compressed’ or anteriorly faced, supero-inferiorly elongated triangular area.

The shape of the palate is parabolic, and brachystaphylin or broad [41], with a breadth:length index of 93.8 (Fig 3). In sharp contrast to the modest anterior protrusion of the upper face suggested from the above structure, the subnasal part of the palate exhibits strong alveolar prognathism: in fact, subnasal prognathism is extreme (large of Larnach and Macintosh [47]).

The four characteristics italicised above reflect a morphology similar to that of Aboriginal Australians rather than to Europeans or East Asians [47]. As detailed in Table 6, based on the available comparative data, about 16% of Melanesians, 11% of Aboriginal Australians, and 5% of Island Southeast Asians equate with Maros-LBB-1a in presenting a broadly Australo-Melanesian morphology on all these four characters. Of the six Gua Cha crania with all of these characters intact, two of them (both Neolithic) also present a consistently Australo-Melanesian morphology [40].

Table 5. Periodontal disease (after [44]) across the Maros-LBB-1a right maxilla.

| Tooth site       | Classification                      | Location     | Classification |
|------------------|-------------------------------------|--------------|----------------|
| Central incisor  | Marked resorption of the alveolar crest | Buccal       | Reactive bone  |
| Lateral incisor  | Marked resorption of the alveolar crest | Buccal       | Reactive bone  |
| Canine           | Marked resorption of the alveolar crest | Buccal       | Reactive bone  |
| First premolar   | Marked resorption of the alveolar crest | Buccal and lingual | Marked resorption of the alveolar crest |
| Second premolar  | Reactive bone                        | Lingual      | Reactive bone  |
| First molar      | Irregular alveolar crest            | Lingual      | Irregular alveolar crest |
| Second molar     | Pockets                             | Buccal       | None           |
| Third molar      | Irregular alveolar crest            | Buccal       | Pockets        |

https://doi.org/10.1371/journal.pone.0257273.t005
Determining an affinity for the Gua Cha remains either with recent, local Island Southeast Asian populations or with Australo-Melanesian populations to the southwest proved exceptionally problematic [40], which invokes the caution recommended by Cunha and Ubelaker [59] in proposing ancestry based on conflicting or inadequate evidence. If this caution is appropriate for a sub-recent, well sampled series with several complete to semi-complete skulls, such as Gua Cha, it logically applies with even greater force to the highly fragmentary and much older Maros-LBB-1a remains.

Discussion

The present scarcity of Late Pleistocene AMH skeletal remains in Wallacea means that our knowledge of the pattern and timing of the initial migration of our species into the region, and later interisland movements, is limited [2,60]. In prior decades, and continuing today, most attempts to model the earliest colonisation of the region by AMH have been based on the so-called ‘two-layer’ hypothesis or model. According to this concept, the first AMH to enter Wallacea at least 50 ka were Australo-Melanesians [61: p119]–direct lineal ancestors of modern-day Aboriginal Australians and Melanesians/Papuans [2,14]. The model holds that, once this founding population reached Sahul, it became cut-off and isolated in this continent until the middle Holocene period [62]. At this stage, direct contact with an as-yet unknown human population is indicated by the human-mediated dispersal of the dingo (Canis dingo) to mainland Australia, a wild canid that may have originally been introduced by Asian seafarers as a fully domesticated dog [63]. According to the two-layer model, the mainland East Asian affinity of modern people in the Philippines, Sulawesi, and islands to the west is due to the arrival ~5–4 ka of Neolithic farmers (‘Austronesians’) from a home base in southern China/Taiwan, and their absorption of the original Australo-Melanesians [64]. In this view, the Malayan-Papuan Line would mainly reflect the eastern limit of the immigrant farmers’ absorption of the pre-Austronesian inhabitants.

More complex models have also been proposed, with implications for a Pleistocene ancestry of the Malayan-Papuan Line. For instance, Karafet et al. [14] contend that following the initial peopling of Sahul by Australo-Melanesians Wallacea was the recipient of later migration events involving Late Pleistocene AMH colonists spreading out of Sunda from source.
populations with different genetic ancestry, and which never made it to Sahul. Claims have also been made for the presence of East Asian AMH populations in Sunda by around 40 ka [60; see also 65], as well as migrations of mainland East Asians into Wallacea during the LGM, a period of time when a combination of environmental changes affecting human subsistence and lower sea levels enhancing interisland visibility may have led to increased human population movements [2]. In a recent model, Curnoe et al. [60] propose that: 1) AMH of African origin reached southern China by 80 ka [66] and from there migrated into northern Sunda (present-day Borneo) and across the Wallace Line to Sulawesi, and possibly to Maluku, but did not extend their range into Sahul. Based on Curnoe et al.’s [60] reanalysis of the Niah Cave ‘Deep Skull’ (~37 ka), the oldest H. sapiens fossil known from Borneo, it is proposed that this early AMH group had a close morphological affinity with present-day mainland East Asians; and 2) a separate wave of AMH colonists of Australo-Melanesian affinity migrated eastward along the southernmost edge of Sunda and dispersed along the southern route across Wallacea into Sahul. According to this model, contrary to the two-layer hypothesis there was no major turnover in biological populations associated with the transition from foraging to farming in Island Southeast Asia: ‘Instead, it seems more likely that Austronesian speakers from Taiwan and island Southeast Asia share a common origin going back to the Late Pleistocene with only a limited signal of the “Out-of-Taiwan” expansion during the Neolithic period’ [60: p15].

As noted, the human skeletal remains from Leang Bulu Bettue dated to ~25–16 ka are the first fossil evidence of hominins recovered thus far from Pleistocene Sulawesi, a key island in our understanding of the pattern of AMH colonisation of Wallacea and Sahul. For what it is worth, these highly fragmentary materials present characters that would be consistent with either an Australo-Melanesian or an Island Southeast Asian affinity, and so this specimen cannot be considered as providing empirical support for either the two-layer model or any of its contenders.

In summary, the two-layer hypothesis holds that the original founding wave of Australo-Melanesians that colonised Wallacea in the Late Pleistocene gave rise to localised island populations that remained isolated genetically and culturally over tens of thousands of years until the arrival of East Asian farmers (‘Austronesians’) in the middle Holocene. It has also been proposed that, following the initial peopling of Sahul by Australo-Melanesians, Wallacea was the recipient of further Late Pleistocene migration events involving AMH spreading into the region from sources in mainland East Asia and intermingling with established Australo-Melanesian populations. Presently, using only the fossil record to go by, it is difficult to test these scenarios on a regional scale and across the known time span of Late Pleistocene occupation of Wallacea by AMH, owing to the scarcity of human skeletal materials in the region. Genomic analyses of living people and ancient DNA sequences are advancing our knowledge of early human migrations and population histories in the region (e.g., Lipson et al. [67]; McColl et al. [68]); thus far, however, there are no ancient human genetic materials from Wallacea (including Maros-LBB1a) and hence our understanding of how the modern pattern of human genetic diversity in the region arose, including the origins of the Malayan-Papuan Line, is poorly developed.

Finally, it is worth us highlighting that the Leang Bulu Bettue individual possibly belonged to the population responsible for one of the world’s oldest known rock art traditions. As mentioned above, dated parietal art in the surrounding Maros-Pangkep karsts spans the time period from at least 45.5 ka until the LGM. The human remains came from Layer 4a, a rich archaeological horizon that yielded diverse and regionally unique evidence for portable art, as well as personal ornaments and pigment use [10]. The former includes small rocks engraved with abstract markings, and, in two cases, figurative imagery [33]. These art objects and ornaments were created long after the most likely initial period of settlement of Wallacea by AMH (~70–50 ka). However, coupled with the U-series rock art dates from Maros-Pangkep, they
suggest that a sophisticated artistic culture existed in South Sulawesi from at least 45.5 ka until around the time of the LGM. Similarly, one Tron Bon Lei burial (from Test Pit B) was interred with elaborately crafted shell fishhooks [11], highlighting the importance of symbols in the lives of Late Pleistocene AMH in Alor and perhaps within the cultural worlds of ‘ice age’ communities in Wallacea generally [10,69].

Conclusion

There are many unknowns in our understanding of the early history of our species in Wallacea. Given the dearth of fossil data, the recovery of any new AMH skeletal element from Pleistocene Wallacea, even highly fragmentary remains like the right maxilla Maros-LBB-1a from Leang Bulu Bettue, is of value; at least to the extent of demonstrating the presence of early H. sapiens in a region that may have been host to multiple species of archaic hominins. The specimen also has the advantage of being securely dated by a variety of chronometric techniques to ~25 to 16 ka. The first modern humans to reach Sulawesi produced some of the oldest known dated rock art [13,30], yet little is known about the origin and cultural lives of these Late Pleistocene hunter-gatherers. Maros-LBB-1a provides us with the first direct fossil insight into the identity of these ancient foragers, and its unusual tooth wear and oral pathology offer tantalising hints on how they adapted to their rainforest environment. It is clear that much more basic fieldwork remains to be done, however, in order to unravel the cultural and biological history of early AMH in this Wallacean island.

Supporting information

S1 Fig. 3D Photoscan model of Maros-LBB-1a. Credit: D.P. McGahan.
(PDF)

Acknowledgments

The Indonesian field research was conducted in collaboration with counterpart institution Pusat Penelitian Arkeologi Nasional (ARKENAS), Jakarta, Indonesia. Other key participating organisations in Indonesia included Balai Arkeologi Sulawesi Selatan (Makassar), Balai Pelestarian Cagar Budaya (Makassar), Departemen Arkeologi Fakultas Ilmu Budaya, Universitas Hasanuddin (Makassar) and Jurusan Arkeologi Fakultas Ilmu Budaya, Universitas Halu Oleo (Kendari). Special acknowledgments go to ARKENAS Director I. Made Geria and Head of Balai Arkeologi Sulawesi Selatan, Irfan Mahmud. We acknowledge Faye Liu and Tara Clark for processing stalagmite samples for U-series dating. We also thank Salmia, Akin Duli, Suryatman, Hasliana, Laode Aksa, Rustan Lebe, Abdullah, Andi Jusdi, Nur Ihsan Djindar, Yinika Perston, Kim Newman, Michelle Langley, Dian Riseley and Zhihong Xu for their support. Tanya Smith, Clark Larsen, Peter S. Ungar, Christopher Schmidt, and Melandri Vlok provided specialist advice on the Maros-LBB-1a dental wear pattern, for which we are grateful.

Author Contributions

Conceptualization: Adam Brumm, Budianto Hakim, Adhi Agus Oktaviana.

Data curation: Adam Brumm, Budianto Hakim, Adhi Agus Oktaviana, Ratno Sardi.

Formal analysis: Adam Brumm, David Bulbeck, Budianto Hakim, Jian-xin Zhao, Maxime Aubert, Yousuke Kaifu.

Funding acquisition: Adam Brumm.
Investigation: Adam Brumm, David Bulbeck, Budianto Hakim, Basran Burhan, Adhi Agus Oktaviana, Iwan Sumantri, Jian-xin Zhao, Maxime Aubert, Ratno Sardi, David McGahan, Andi Muhammad Saiful, Shnatria Adhityatama, Yousuke Kaifu.

Methodology: Adam Brumm, David Bulbeck, Budianto Hakim, Basran Burhan, Jian-xin Zhao.

Project administration: Adam Brumm, Budianto Hakim, Basran Burhan, Adhi Agus Oktaviana, Iwan Sumantri, Shnatria Adhityatama.

Resources: Adam Brumm, Budianto Hakim, Adhi Agus Oktaviana, Iwan Sumantri.

Supervision: Adam Brumm, Budianto Hakim, Basran Burhan, Iwan Sumantri.

Validation: Adam Brumm.

Visualization: Adam Brumm, David Bulbeck, Budianto Hakim, Basran Burhan, Ratno Sardi.

Writing – original draft: Adam Brumm, David Bulbeck, Budianto Hakim, Maxime Aubert.

Writing – review & editing: Adam Brumm, David Bulbeck, Budianto Hakim, Jian-xin Zhao, Maxime Aubert, David McGahan.

References
1. Détroit F, Dizon E, Falguères C, Hameau S, Ronquillo W, Sémah F. Upper Pleistocene Homo sapiens from the Tabon Cave (Palawan, the Philippines): Description and dating of new discoveries. C.R. Palevol. 2004; 3: 705–712.
2. Samper Carro SC, Gilbert F, Bulbeck D, O’Connor S, Louys J, Spooner N, et al. Somewhere beyond the sea: Human cranial remains from the Lesser Sunda Islands (Alor Island, Indonesia) provide insights on Late Pleistocene peopling of Island Southeast Asia. J. Hum. Evol. 2019; 134: 102638. https://doi.org/10.1016/j.jhevol.2019.07.002 PMID: 31446971
3. O’Connell JF, Allen J, Williams MAJ, Williams AN, Turney CSM, Spooner NA, et al. When did Homo sapiens first reach Southeast Asia and Sahul? Proc. Natl. Acad. Sci. U.S.A. 2018; 115(34): 8482–8490. https://doi.org/10.1073/pnas.1808385115 PMID: 30082377
4. Clarkson C, Jacobs Z, Marwick B, Fullagar R, Wallis L, Smith M, et al. Human occupation of northern Australia by 65,000 years ago. Nature 2017; 547: 306–310. https://doi.org/10.1038/nature22968 PMID: 28726833
5. Bird MJ, Beam RN, Condie SA, Cooper A, Ulm S, Veth P. Palaeogeography and voyage modeling indicates early human colonization of Australia was likely from Timor-Roti. Quat. Sci. Rev. 2018; 191: 431–439.
6. Bird MJ, Condie SA, O’Connor S, O’Grady D, Reepmeyer C, Ulm S, et al. Early human settlement of Sahul was not an accident. Sci. Rep. 2019; 9: 8220. https://doi.org/10.1038/s41598-019-42946-9 PMID: 31209234
7. Birdsell JB. The recalibration of a paradigm for the first peopling of Greater Australia. In: Allen J, Golson J, Jones R, editors. Sunda and Sahul: prehistoric studies in Southeast Asia, Melanesia and Australia, London: Academic Press; 1977. pp. 113–167. https://doi.org/10.14219/jada.archive.1977.0304 PMID: 319134
8. Kealy S, Louys J, O’Connor S. Islands under the sea: a review of early modern human dispersal routes and migration hypotheses through Wallacea. J. I. Coast. Archaeol. 2015. https://doi.org/10.1080/15564894.2015.1119218
9. Kealy S, Louys J, O’Connor S. Least-cost pathway models indicate northern human dispersal from Sunda to Sahul. J. Hum. Evol. 2018; 125: 59–70. https://doi.org/10.1016/j.jhevol.2018.10.003 PMID: 30502698
10. Brumm A, Langley MC, Moore MW, Hakim B, Ramli M, Sumantri I, et al. Early human symbolic behavior in the Late Pleistocene of Wallacea. Proc. Natl. Acad. Sci. U.S.A. 2017; 114(16): 4105–4110. https://doi.org/10.1073/pnas.1619013114 PMID: 28373568
11. O’Connor S, Mahirta S, Samper Carro C, Hawkins S, Kealy S, Louys J, et al. Fishing in life and death: Pleistocene fish-hooks from a burial context on Alor Island, Indonesia. Antiquity 2017; 91(360): 1451–1468.
12. Hawkins S, O’Connor S, Maloney TR, Litster M, Kealy S, Fenner JN, et al. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. Quat. Sci. Rev. 2017; 171: 58–72.

13. Brumm A, Oktaviania AA, Burhan B, Hakim B, Lebe R, Zhao J-X, et al. Oldest cave art found in Sulawesi. Sci. Adv. 2021; 7(3): eabd4648. https://doi.org/10.1126/sciadv.abd4648 PMID: 33523879

14. Karafet TM, Hallmark B, Cox MP, Sudoyo H, Downey S, Lansing JS, et al. Major east–west division underlies Y chromosome stratification across Indonesia. Mol. Bio. Evol. 2010; 27(8): 1833–1844. https://doi.org/10.1093/molbev/msq063 PMID: 20207712

15. Brown P, Sutikna T, Morwood MJ, Soejono RP, Jatmiko, Saptomo EW, et al. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature 2004; 431: 1055–1061. https://doi.org/10.1038/nature02999 PMID: 1514638

16. Morwood MJ, Soejono RP, Roberts RG, Sutikna T, Turney CSM, Westaway KE, et al. Archaeology and age of a new hominin from Flores in eastern Indonesia. Nature 2004; 431(7012): 1087–1091. https://doi.org/10.1038/nature02956 PMID: 15510146

17. Sutikna T, Tocheri MW, Morwood MJ, Saptomo EW, Jatmiko, Awe RD, et al. Revised stratigraphy and chronology for Homo floresiensis at Liang Bua in Indonesia. Nature 2016; 532: 366–369. https://doi.org/10.1038/nature17179 PMID: 27027286

18. Detroit F, Mijares AS, Corny J, Daver G, Zanolli C, Dizon E, et al. A new species of Homo from the Late Pleistocene of the Philippines. Nature 2019; 568: 181–186. https://doi.org/10.1038/s41586-019-1067-9 PMID: 30971845

19. van den Bergh GD, Bo Li, Brumm A, Grün R, Yurnaldi D, Moore MW, et al. Earliest hominin occupation of Sulawesi, Indonesia. Nature 2016; 529: 208–211. https://doi.org/10.1038/nature16448 PMID: 26762458

20. Cooper A, Stringer CB. Did the Denisovans Cross Wallace’s Line? Science 2013; 342: 321–323. https://doi.org/10.1126/science.1244869 PMID: 24136958

21. Jacobs GS, Hdadash G, Saag L, Kusuma P, Darusallam CC, Lawson DJ, et al. Multiple deeply divergent Denisovan ancestries in Papuans. Cell 2019; 177: 1010–1021. https://doi.org/10.1016/j.cell.2019.02.035 PMID: 30981557

22. Mondal M, Bertranpetit J, Lao O. Approximate Bayesian computation with deep learning supports a third archaic introgression in Asia and Oceania. Nat. Comm. 2019; 10: 246. https://doi.org/10.1038/s41467-018-08089-7 PMID: 30072539

23. Tucci S, Vohr SH, McCoy RC, Vernot B, Robinson MR, Barbieri C, et al. Evolutionary history and adaptation of a human pygmy population of Flores Island, Indonesia. Science 2018; 361: 511–516. https://doi.org/10.1126/science.aar8486 PMID: 30072539

24. Sarasin P, Sarasin F. Reisen in Celebes II. Wiesbaden: C.W. Kreidel’s Verlag; 1905.

25. McDona ld RC. Limestone morphology in South Sulawesi, Indonesia. Zeitschrift für Geomorphologie 1976; 26(suppl.): 79–91.

26. Aubert M, Brumm A, Ramil I, Sutikna T, Hamil EW, Hakim B, et al. Pleistocene cave art from Sulawesi, Indonesia. Nature 2014; 514: 223–227. https://doi.org/10.1038/nature14222 PMID: 25297435

27. Brumm A, Hakim B, Ramil I, Aubert M, van den Bergh GD, Li Bo, et al. A reassessment of the early archaeological record at Leang Burung 2, a Late Pleistocene rock-shelter site on the Indonesian island of Sulawesi. PLOS ONE. 2018; 13(4): e0193025. https://doi.org/10.1371/journal.pone.0193025 PMID: 29641524

28. Bo Li, Roberts RG, Brumm A, Guo Y-J, Hakim B, Ramil I, et al. IRSL dating of fast-fading sanidine feldspars from Sulawesi, Indonesia. Ancient TL 2016; 34(2): 1–13.

29. Langley MC, Hakim B, Oktaviania AA, Burhan B, Sumantri I, Sulistyar to PH, et al. Portable art from Pleistocene Sulawesi. Nat. Hum. Behav. 2020; 4: 597–602. https://doi.org/10.1038/s41562-020-0837-6 PMID: 32209323
34. Burton JA, Mustari AH, Rejeki IS. Sulawesi Warty Pig *Sus celebensis* (Muller & Schlegel, 1843). In: Mellett M, Meijaard E, editors. Ecology, conservation and management of wild pigs and peccaries. Cambridge: Cambridge University Press. 2018; pp. 184–192.

35. Zhou HY, Zhao JX, Wang Q, Feng YX, Tang J. Speleothe m-derived Asian summe r monsoon variations in Central China during 54–46 ka. J. Quat. Sci. 2011; 26: 781–790.

36. Clark TR, Zhao J-x, Roff G, Feng Y-x, Done TJ, Nothdurft LD, et al. Discer ning the timing and cause of historical mortality events in modern Porites from the Great Barrier Reef. Geochim. Cosmochim. Acta. 2014; 138: 57–80. https://doi.org/10.1016/j.gca.2014.04.022

37. Ludwig KR. User’s manual for Isoplot 3.75, a geochronolog ical toolkit for Microsof t Excel. Berkeley: Berkeley Geochronology Center; 2012.

38. Cheng H, Edwards RA, Hof J, Gallup CD, Richards DA, Asmerom Y. The half-lives of uranium-234 and thorium-230. Chem. Geol. 2000; 169: 17–33.

39. Hogg AG, Heaton T, Hua Q, Palmer J, Turney C, Southo n J, et al. SHCal20 Southern Hemisphere cali bration, 0–50,000 Years cal BP. Radiocarbon 2020; 62(4): 759–778.

40. Bulbeck D. The Gu Cha burials. In Zuraina M, editor. The Perak Man and other prehistoric skeletons of Malaysia. Penang: Penerbit Univers iti Sains Malaysia; 2005. pp. 253–309. https://doi.org/10.1126/science.1109792 PMID: 15890885

41. Bräuer G. Osteometrie: a. Kraniometri e. In: Knußman R, editor. Lehrbuch der anthropo logie. Band I. Wesen und methoden der anthropologie. 1. Teil. wissensc haftstheorie, geschic hte, morphologis chen methoden. Stuttgart: Gustav Fischer Verlag; 1988. pp. 160–192.

42. Howells WW. Skull shapes and the map: craniome tric analyses in the dispersion of modern Homo. Papers of the Peabody Museum of Archaeology and Ethnology. Cambridge, MS: Harvard University; 1989.

43. Patterson DK Jr. A diachronic study of dental palaeopathology and atritional status of prehisto ric Ontario pre-Iroquo is and Iroquois populations. Ottawa: National Museums of Canada; 1984.

44. Tayles N. The people. The excavation of Khok Phano m Di: a prehistoric site in central Thailand (Vol 5). London: Society of Antiquarie s; 1999.

45. Scott GR, Turner CG II. The anthropolog y of modern human teeth: dental morphology and its variation in recent human populations. Cambridge: Cambridge University Press; 1997.

46. Hillson S. Dental anthropology. Cambridge: Cambridge University Press; 1996.

47. Larnach SL, Macintosh NWG. The craniology of the Aborigine s of Queens land. Oceania Monographs No. 15. Glebe: Australasia Medical Pub. Co; 1970.

48. Kaifu Y, Baba H, Sutikna T, Morwood MJ, Kubo D, Saptomo EW, et al. Craniofacial morphology of *Homo floresiensis*: description, taxonomic affinities, and evolutionary implication. J. Hum. Evol. 2011; 61: 644–682. https://doi.org/10.1016/j.jhevol.2011.08.008 PMID: 22036083

49. Kaifu Y, Kono RT, Sutikna T, Saptomo EW, Jatmiko, Due Awe R. Unique dental morpho logy of *Homo floresiens is* and its evolutionary implication s. PLoS ONE 2015; 10(11): e0141614. https://doi.org/10.1371/journal.pone.0141614

50. Kaifu Y, Kono R, Sutikna T, Saptomo EW, Jatmiko, Due Awe R, et al. Descriptions of the dental remains of *Homo floresiens is*. Anthropological Science 2015; 123(2): 129–145.

51. Chen F, Welker F, Shen C-C, Bailey SE, Bergmann I, Davis S, et al. A late Middle Pleistocen e Deniso van mandible from the Tibetan Plateau. Nature 2019; 569: 409–412. https://doi.org/10.1038/s41586-019-1139-x PMID: 31043746

52. Larnach SL, Freedman L. Sex determination of Aboriginal crania from coastal New South Wales. Records of the Australian Museum 1964; 26: 295–308.

53. O’Connor S, Bulbeck D, Piper PJ, Aziz F, Marwick B, Campos F, et al. The human occupation record of Gua Mo’o hono shelter, Towuti-Route region of southeastern Sulawesi. In: O’Connor S, Bulbeck D, Meyer J, editors. The archaeology of Sulawesi: current research on the Pleistocene to the historic period. Terra Australis 48. Canberra: ANU Press; 2018. pp. 117–151. https://doi.org/10.22459/TA48.11.2018

54. O’Connor S, Aziz FA, Marwick B, Fenner J, Prasetyo B, Bulbeck D, et al. Final report on the project “The archaeology of Sulawesi: a strategic island for understanding modern human colonization and interactions across our region”. Report to Indonesia’s State Ministry of Research and Technology, Department of Archaeology and Natural History, Australian National University, Canberra and Department of Prehistory, Indonesia’s National Centre for Archaeological Research and Development, Jakarta; 2014.

55. Gilmore CC. A comparison of antemortem tooth loss in human hunter-gatherers and non-human catar rhines: implications for the identification of behavioral evolution in the human fossil record. Am. J. Phys. Anthropol. 2013; 151: 252–264. https://doi.org/10.1002/apa.22275 PMID: 23640546
56. Humphrey LT, De Groote I, Morales J, Barton N, Collett S, Bronk Ramsey C, et al. Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. Proc. Natl. Acad. Sci. U.S.A. 2014; 111(3): 954–959. https://doi.org/10.1073/pnas.1318176111 PMID: 24395774

57. Alt KW, Pichler SL. Artificial modifications of human teeth. In: Alt KW, Rösing FW, Teschler-Nicola M, editors. Dental anthropology: fundamentals, limits, and prospects. New York, NY: Springer; 1998. pp. 387–415.

58. Bulbeck D. Dental morphology at Gua Cha, West Malaysia, and the implications for “Sundadonty”. Bulletin of the Indo-Pacific Prehistory Association 2000; 19: 17–41.

59. Cunha E, Ubelaker DH. Evaluation of ancestry from human skeletal remains: a concise review. Forensic Sci. Res. 2020; 5(2): 89–97. https://doi.org/10.1080/20961790.2019.1697060 PMID: 32939424

60. Curnoe D, Datan I, Taçon PSC, Ung CLM, Sauffi MS. Deep Skull from Niah Cave and the Pleistocene peopling of Southeast Asia. Front. Ecol. Evol. 2016; 4. https://doi.org/10.3389/fevo.2016.00115 PMID: 28758093

61. Bellwood P. First Islanders. Hoboken: Wiley; 2017.

62. Matsumura H, Yoneda M, Dodo Y, Oxenham MF, Cuong NI, Thuy NK, et al. Terminal Pleistocene human skeleton from Hang Cho Cave, northern Vietnam: implications for the biological affinities of Hoabinhian people. Anthropological Science. 2008; 116(3): 201–217.

63. Balmé J, O’Connor S, Fallon S. New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. Sci. Rep. 2018; 8: 9933. https://doi.org/10.1038/s41598-018-28324-x PMID: 30026564

64. Matsumura H, Hung H-C, Higham C, Zhang C, Yamagata M, Nguyen LC, et al. Cranio metrics reveal “two layers” of prehistoric human dispersal in eastern Eurasia. Sci. Rep. 2019; 9: 1451. https://doi.org/10.1038/s41598-018-35426-z PMID: 30723215

65. Aubert M, Setiawan P, Oktaviana AA, Brumm A, Sulistyarto PH, Saptomo EW, et al. Palaeolithic cave art in Borneo. Nature 2018; 564: 254–257. https://doi.org/10.1038/s41586-018-0679-9 PMID: 30405242

66. Wu L, Martín-Torres M, Cai Y-j, Xing S, Tong H-w, Pei S-w, et al. The earliest unequivocally modern humans in southern China. Nature 2015; 526: 696–700. https://doi.org/10.1038/nature15696 PMID: 26466566

67. Lipson M, Cheronet O, Mallick S, Rohland N, Oxenham M, Pietrusewsky M, et al. Ancient genomes document multiple waves of migration in Southeast Asian prehistory. Science 2018; 361: 2–95. https://doi.org/10.1126/science.aat3188 PMID: 29773666

68. McColl H, Racimo F, Vinner L, Demeter F, Gakuhari T, Moreno-Mayar JV, et al. The prehistoric peopling of Southeast Asia. Science 2018; 361: 88–92. https://doi.org/10.1126/science.aat3628 PMID: 29976827

69. Langley MC, Clarkson C, Ulm S. Symbolic expression in Pleistocene Sahul, Sunda, and Wallacea. Quat. Sci. Rev. 2019; 221: 105883.