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# The youngest *stegodon* remains in Southeast Asia from the Late Pleistocene archaeological site Liang Bua, Flores, Indonesia

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**Abstract**

*Stegodon* remains originating from Late Pleistocene layers of the archaeological cave site Liang Bua on the Indonesian Island of Flores, are described as a new endemic dwarf subspecies: *Stegodon florensis insularis* subsp. nov. Some fossil *Stegodon* fragments were found in association with the recently described remains of *Homo floresiensis,* but many occur in levels with high artefact concentrations. The direct ancestor is the larger-sized *S. florensis florensis,* known from Early Pleistocene and early Middle Pleistocene sites on Flores. The assemblage from Liang Bua comprises mostly dental and skeletal elements of juvenile individuals. *S.f. insularis* is characterized by an advanced molar ridge formula and diminutive size: on average the molars are 30 per cent smaller in linear dimensions as compared to the ancestral species. Hominin activities are likely to have played a role in the *Stegodon* bone accumulation at Liang Bua.


## 1. Introduction

Two *Stegodon* species have previously been described from the Soa Basin, on the East Indonesian island of Flores. Firstly, *Stegodon sondaari* (van den Bergh, 1999), a dwarfed species with an adult body weight of around 300 kg from the 900 kyr-old site of Tangi Talo, and secondly, the intermediate to large-sized *Stegodon florensis* from various stratigraphically younger sites, such as Dozu Dhalu, Mata Menge, Boa Lesa and Kobatuwa, which date between 850 and 700 ka (Morwood et al., 1998). The latter species was initially described by Hooijer (1957) as a subspecies of *Stegodon trigonocephalus*, known from Early and Middle Pleistocene sites on Java. However, additional fossil finds from the Soa Basin, collected between 1992 and 1994, justified its classification as a distinct species, *S. florensis*, with an estimated average adult body weight of ca. 850 kg. *S. trigonocephalus* from Java, of which three chrono-subspecies have been distinguished, is larger than *S. florensis* though the smallest individuals (from the locality Trinil) tend to overlap in size with the largest *S. florensis* individuals. *S. trigonocephalus* has an estimated bodyweight based on femur length of between 1017 and 1713 kg. However, *S. trigonocephalus* was not necessarily the direct ancestor of *S. florensis*, which may have arrived from the north via Sulawesi (van den Bergh, 1999).

Here we describe a new *Stegodon* subspecies from Flores, *S. florensis insularis* subsp. nov., excavated between 2001 and 2004 from Late Pleistocene deposits at Liang Bua, a limestone cave in West Flores. This subspecies was intermediate in size between *S. sondaari* and *S. florensis* from the Soa Basin. At Liang Bua, evidence for *S.f. insularis* dates to between 95 and 12 ka, and is associated with high concentrations of stone artefacts and the skeletal remains of *Homo floresiensis*, an endemically dwarfed hominin species (Brown et al., 2004; Morwood et al., 2005). Cut marks on some of the *Stegodon* bones and their distribution in relation to stone artefacts on occupation floors suggest that the animals at the site were butchered by hominins (Morwood et al., 2004, 2005).

At 12 ka the Liang Bua population of *Stegodon* is the most recent credible occurrence for stegodonts in Southeast Asia. In South China *Stegodon* continues into the

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Holocene locally, as evidenced by the finds from the Neolithic site Xiaohe Cave, which has been dated at 4100 BP (Ma and Tang, 1992). In Java, stegodonts were eventually fully replaced by the modern Asian elephant (*Elephas maximus*) at the onset of the last interglacial between 120 and 130 ka (van den Bergh et al., 2001a; Storm et al., 2005; Westaway et al., under review). The disappearance of *Stegodon* from the Liang Bua sequence coincides with a layer of fine-grained white tuff deposited in the cave around 11 ka. The associated volcanic eruption and environmental disruption may have been a factor in the extinction of both *Stegodon* and *H. floresiensis*.

## 2. Materials and methods

### 2.1. Institutional abbreviations

ICA, Indonesian Centre for Archaeology in Jakarta; GRDC, Geological Research and Development Centre in Bandung; NHMN, Natural History Museum NATURALIS in Leiden.

### 2.2. Excavation procedure

Between 2001 and 2004 the Pleistocene deposits of Liang Bua were excavated in five sectors (I, III, IV, VII and XI), varying in size between $2\times2$ and $3\times3\,m^2$ (Fig. 1). Previous excavations carried out by Soejono (1980, 1985) had not reached bedrock and did not penetrate into the Pleistocene sequence. Excavations took place in 10 cm spits or followed stratigraphic boundaries (e.g. "spit 20" means "from a depth of between 190 and 200 cm"). A more detailed description of the excavation and dating procedures is given elsewhere (Morwood et al., 2004, 2005).

### 2.3. Anatomical terms, measurements and abbreviations

The terminology and the parameters used in this paper are the same as those described in Van den Bergh (1999) and are briefly repeated in the appendix.

### 2.4. Material

*Stegodon* remains have been recovered from Late Pleistocene deposits in sectors I, III, IV, VII and XI of the archaeological excavations at Liang Bua (Fig. 1). In total, 220 identifiable *Stegodon* remains (Number of Individual Specimens (NISP) = 220) were recovered, amongst the hundred thousands of fossils, mostly attributable to 6 or 7 species of muridae, but also including *Varanus komodoensis*, *Varanus hooijeri*, *H. floresiensis*, birds, bats, insectivores, frogs and fish. Amongst the identifiable *Stegodon* remains, 149 specimens comprise dental elements (including those in situ in mandible or maxilla fragments; cranial fragments with two milkmolars counted as single specimens), which is 67.7 per cent of the total *Stegodon* NISP. Of these dental elements, 69 molar

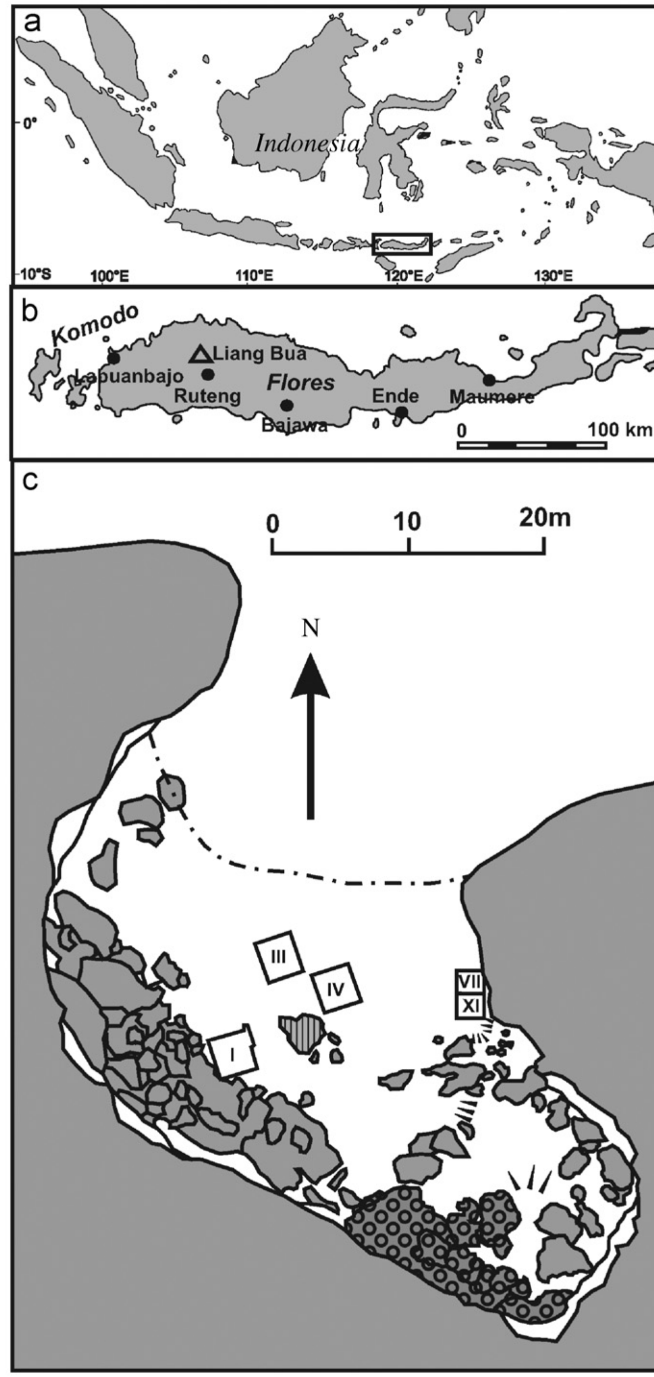


Fig. 1. (a) Location of Flores in Indonesia, (b) location of Liang Bua in Flores and (c) horizontal plan of the excavations carried out in Liang Bua between 2000 and 2004, with the excavated sectors indicated with roman numerals. Grey areas indicate limestone; dotted line marks the boundary of the cave ceiling; vertical dashed limestone marks a large stalagmitic structure in the centre of the cave; circled pattern marks a cemented conglomerate attached to the cave wall and deposited during the initial infill history of the cave.

specimens are complete enough to allow identification of the molar rank (31.4 per cent of NISP). In addition, there are 13 milk tusks (or tushes) and 23 permanent tusk fragments, of which the largest fragment is 280 mm long, but most specimens representing small fragments.

The remaining dental specimens ($n = 38$) are small molar fragments or just isolated molar ridges or even small ridge fragments, of which only the distinction between molar or milkmolar could be made based on the enamel thickness (ET). The minimum number of individuals (MNI) of the assemblage is 47 individuals, based on the assignment of each identifiable molar element and its wear stage to one of in total 43 dental wear age classes (van den Bergh, 1999) in combination with the stratigraphic positions. Molar fragments with the same dental wear age class but of opposite and/or opposing quadrants wear assigned to a single individual, unless vertically occurring more than 30 cm apart in the stratigraphic column. All dental specimens are listed in the appendix (Table A1).

Forteen milkmolars are still embedded in 8 maxilla and 2 mandible fragments (Table A2). Many skull fragments consist of tiny pieces of pneumatic bone, identifiable as elephantoid cranial vault fragments. These have not been included in the counts. There are 12 isolated petrosals (os petrosum). Larger portions of skull are rare, but include two juvenile parietals and a juvenile squamosal. There are 45 identifiable postcranial fragments including bones of pes and manus, vertebrae, scapulae, radii, tibiae, femurs and a pelvis. None of the long limb bones is complete. These counts do not include small juvenile costa fragments. Identifiable postcranial parts are listed in the appendix (Table A3). The representation of skeletal elements is depicted in Fig. 2.

There were few *Stegodon* finds in sector I, which is the most to the southwest located sector where the fossil-bearing layers only extend to a depth of 2.6 m (one maxilla fragment with $dP^3$, four isolated (milk) molars and one milktusk or tush). Sector III also yielded few finds (three (milk)molar fragments of uncertain rank and a single phalanx fragment). From sector IV were recovered 26 identifiable molars, seven tushes, 13 skull fragments and 19 postcranial elements. Most *Stegodon* remains originate from the eastern part of the cave. Sector VII yielded 33 dental specimens, two skull fragments and four postcranials. The finds from sector VII are generally of a very poor preservation (one maxilla fragment with $dP^2$ and $dP^3$, two tushes and three isolated identifiable molar remains, the remaining part representing small tusk and (milk) molar fragments of uncertain rank), contrasting strongly with the better preserved fossil remains from adjacent sector XI. Sector XI yielded the largest number of 109 identifiable remains, including 38 (milk) molars of which the rank could be ascertained, three tushes, 21 postcranial elements and 20 identifiable cranial fragments (including nine isolated petrosals and two juvenile mandibles). The type specimen, a complete $M_2$, originates from this sector as well.

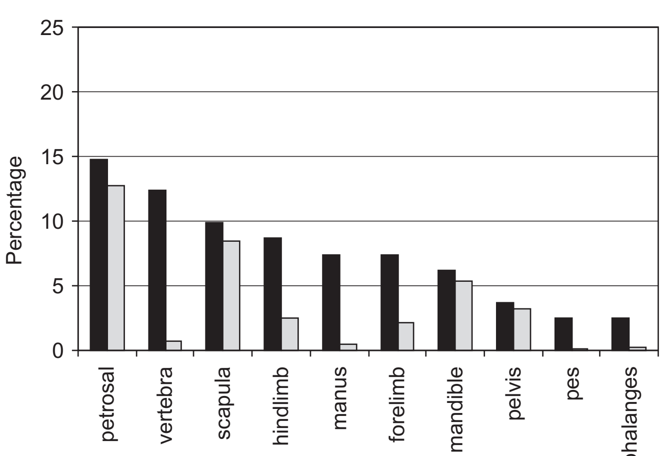


Fig. 2. Representation of skeletal elements. Grey bars: representation as the percentage of total skeletal specimens ($n = 81$; of the skull fragments only the petrosals are plotted in the graph and of the costa only adult specimens including proximal articulation ($n = 1$), have been included in the calculations). Black bars: representation of skeletal elements as percentage of expected amount based on an MNI of 47.

## 3. Stratigraphy

The Pleistocene deposits filling in Liang Bua are predominantly terra rossa clays derived from weathering of limestone, interspersed with rock-fall, conglomerate and (locally cross-bedded) lenses of tuffaceous silts. Layers of flowstone have also been formed locally. The deepest excavation extended down to a depth of 10.4 m in sectors VII and XI, not reaching bedrock. Sector XI (and sector VII immediately to the north) also showed changes over time in the nature of the *Stegodon* evidence. *Stegodon* remains from the deeper levels below 6 m depth are dominated by adult molar and tusk fragments, but higher in the sequence between 4.5 and 5 m depth in sector XI, concentrations of juvenile *Stegodon* bones and molars dominate in a number of stratified "living floors" associated with high concentrations of stone artefacts, fossils of other taxa such as rat, varanid, and bird remains, and dated to ca. 15 ka. Directly to the south in sector VII, in the lateral equivalent of these artefact/bone concentrations, clayey layers slope down towards the cave entrance in the north. These features have been interpreted (Morwood et al., 2005) as an elevated area (sector XI) that sloped down into what must have been a pool with standing water (sector VII). This could explain the overall fragmented nature in sector VII of the *Stegodon* remains, of which the smallest fragments seem to have washed down from the elevated area down-slope into this pool. The relatively complete nature of the LB01 *H. floresiensis* skeleton, which was found partly articulated in the clayey pool sediments at 5.9 m depth, contrasts strongly with the fragmentary nature of the few *Stegodon* remains that seem to have washed down into the pool from the adjacent elevated area (compare Tables A1–A3: sector VII and XI, spits 58–60).

The earlier deposits contain layers of conglomerate indicating periods of stronger water flow, which may have selected for heavier and more durable (full-grown adult bones) faunal fragments. In sector I a flowstone with an age of between 50 and 60 kyr and attached to the west wall of the cave, seals off Pleistocene deposits below. Here the cultural deposits containing *Stegodon* extend to a maximum depth of only 2.6 m, and are underlain by 6 m of sterile, cross-bedded tuffaceous silts and sands. An important marker bed encountered in sectors IV, VII and XI consists of a layer of fine-grained white tuff, which filled in existing relief around the Pleistocene–Holocene transition. The Holocene sequence above this marker bed is horizontally layered. The Pleistocene stratigraphy is rather complex, with evidence for a number of erosional phases followed by infill of existing depressions and channels. Detailed stratigraphic cross-sections of sectors VII and XI are given in Morwood et al. (2004, 2005) and Westaway (2006).

## 4. Systematic palaeontology

Order PROBOSCIDEA Illiger 1811
Superfamily ELEPHANTOIDEA Gray (1821)
Family STEGODONTIDAE Osborn (1918)
Genus *STEGODON* Falconer (1857)
Species *STEGODON FLORENSIS* Hooijer (1957)
*STEGODON FLORENSIS INSULARIS* SUBSP. NOV.

### 4.1. Derivatio nominis

Recognizing that this subspecies evolved in isolation on an island.

### 4.2. Holotype

The designated type specimen is a complete and slightly worn lower dextral $M_2$ that was excavated in 2004 from 4.5 m depth in sector XI, Liang Bua. The repository is the Indonesian Centre for Archaeology in Jakarta (ICA no. 456; Plate 2, fig. 3).

### 4.3. Referred material

All other *Stegodon* dental, cranial and postcranial fossils from Liang Bua described in this paper and listed in the appendix. The repository is the ICA.

### 4.4. Diagnosis

A small-sized *Stegodon* with linear dimensions intermediate between *S. sondaari* and *S.f. florensis* and comparatively narrow molars. The ridge-crest formula of the molars is very advanced for *Stegodon* and is as follows:

$$\mathrm{dP2}\frac{0-3}{1-2},\quad \mathrm{dP3}\frac{5-6}{6-7},\quad \mathrm{dP4}\frac{7}{8},$$

$$\mathrm{M1}\frac{\text{-}8}{8},\quad \mathrm{M2}\frac{6\text{-}}{12},\quad \mathrm{M3}\frac{\text{-}9}{\text{-}}.$$

The molars are rather hypsodont for *Stegodon*, a feature not uncommon for island stegodonts. Hypsodonty indices of upper milk molars vary between 48 and 80, and of lower milk molars between 59 and 86; and for upper molars between 67 and 88 and for lower molars between 76 and 93. The maximum width of the ridges occurs at the base, with convex lateral and medial borders convergent in apical direction. Conules of ridges are rather blunt. A median cleft is usually strongly developed in the milk molars, and occurs more frequently in mandibular specimens. Delicate scalloped enamel folding in the milk molars, with relatively high amplitude wrinkling is seen.

### 4.5. Differential diagnosis

*S.f. insularis* differs from *S. sondaari*, van den Bergh 1997 and *Stegodon timorensis* Sartono (1969) in having molars that have linear dimensions 20–70 per cent larger, more ridges on the dP3 and dP4 and relatively thinner, more folded enamel. The molars of *S.f. insularis* differ from *S.f. florensis* Hooijer (1957) by being on average 30 per cent smaller in linear dimensions and having a more advanced plate formula. *S. trigonocephalus* Martin (1887), from Java, has larger molars with lower L/W and H/W indices. *S. sompoensis* Hooijer (1964) is of comparable size, but like *S. trigonocephalus*, has lower L/W indices of homologue dental elements and less ridges per homologue molar. Except for island stegodonts such as *S.f. florensis*, *S. timorensis* and *S. aurorae*, the molar ridges of continental stegodonts are less hypsodont than in *S.f. insularis*. All mainland *Stegodon* species are larger, and have distinct, less advanced molar ridge formulas.

### 4.6. Locality

Liang Bua is a limestone cave located 13 km northwest of Ruteng, the regional capital of Manggarai Regency, West Flores, at an altitude of 500 m above sea level and at 30 km distance from the North Coast (S 08°31′50.4″, E 120°26′36.9″). The cave entrance lies 30 m above and 200 m south of the Wae Racang River.

### 4.7. Horizon and age

The youngest *S.f. insularis* remains at Liang Bua occur just below the white tuffaceous silt that is bracketed by radiocarbon ages of 13.1 and 10.7 calibrated ka (Morwood et al., 2004). More specifically, sector XI, yielded a dextral $dP_3$ at 3.2 m depth with an inferred age of 12 ka, while the holotype $M_2$ from 4.5 m depth is directly associated with charcoal with a calibrated ABOX.SC radiocarbon age of 13.1 ka. The oldest dated *S.f. insularis* remains are from 7.5 m depth in sector IV, where sediments yielded an OSL age of $95 \pm 12.53$ ka. From the same sector, a *Stegodon* molar from 4.5 m depth yielded a coupled ESR/uranium-series age of $74+14-12$ ka (Morwood et al., 2004).

## 5. Description of the material

Most dental and skeletal elements are from juvenile individuals. Table A1 in the appendix lists all dental elements together with their measurements. The excavation sectors and spit levels of all fossils specimens are also indicated in the appendix. Summary measurements, including the minimum, maximum and average measurements of all dental elements are given in Table 1.

### 5.1. Dental elements

*$dI^2$*. $n = 13$ (nine with complete enamel crowns). The deciduous incisors, or milk tusks (also known as tushes) are well represented in the Liang Bua collection. They are characterized by a blunt enamel crown with an oval cross-section. Tushes of *Mammuthus primigenius* also have an oval cross-section, the longer diameter corresponding with the vertical and the shorter diameter with the horizontal

Table 1
Summary measurements of *Stegodon florensis insularis* subsp. nov. molars from Liang Bua

| | | *P* | *P* | *L* | *W* | *H* | LF | *L/W* | ET | *h/w* |
|---|---|---|---|---|---|---|---|---|---|---|
| $dP^2$ | Average | 0/2x/x2x/3/3x | 2.25 | 10.8 | 12.3 | 8.8 | — | 0.88 | | 76.8 |
| Sup. | Min | | 0 | 9.0 | 10.0 | 8 | — | 0.74 | 0.9 | 67.2 |
| | Max | | 3 | 12.2 | 13.9 | 10.2 | — | 0.98 | 1 | 82.3 |
| | SD | | 1.04 | 0.98 | 1.31 | 1.24 | — | 0.09 | | 8.37 |
| | CV | | 47.44 | 9.38 | 10.93 | 15.35 | — | 10.51 | | 11.80 |
| | *n* | | 8 | 9 | 9 | 3 | — | 9 | | 3 |
| $dP_2$ | Average | 1/x1/2 | 1.4 | 9.66 | 11.54 | 9.5 | — | 0.84 | | 83.4 |
| Inf. | Min | | 1 | 7.6 | 10 | 8.1 | — | 0.76 | | 80.0 |
| | Max | | 2 | 10.8 | 12.3 | 10 | — | 0.89 | | 91.0 |
| | SD | | 0.55 | 1.37 | 1.05 | 0.93 | — | 0.05 | | 5.10 |
| | CV | | 41.08 | 14.86 | 9.51 | 10.45 | — | 6.42 | | 6.50 |
| | *n* | | 5 | 5 | 5 | 4 | — | 5 | | 4 |
| $dP^3$ | Average | x5x/6x/x6x | 5.9 | 44.5 | 29.2 | 15.5 | 13.2 | 1.53 | — | — |
| Sup. | Min | | 5 | 40.0 | 26.5 | 13.6 | 12.2 | 1.38 | 0.9 | 48.0 |
| | Max | | 6 | 49.3 | 32.5 | 17.0 | 14.3 | 1.63 | 2.0 | 71.0 |
| | SD | | 0.33 | 2.7 | 1.7 | 1.1 | 0.6 | 0.1 | | |
| | CV | | 5.73 | 6.1 | 5.8 | 7.5 | 4.7 | 5.5 | | |
| | *n* | | 17 | 14 | 20 | 8 | 17 | 13 | 12 | 7 |
| $dP_3$ | Average | x6x/7x/x7/x7x | 6.9 | 48.0 | 25.8 | 16.3 | 13.9 | 1.85 | | |
| Inf. | Min | | 6 | 45 | 25 | 15 | 13 | 1.78 | 1.2 | 59.0 |
| | Max | | 7 | 51.4 | 27.2 | 16.7 | 15.1 | 1.95 | 1.7 | 86.0 |
| | SD | | 0.30 | 1.86 | 0.86 | 0.61 | 0.88 | 0.06 | | |
| | CV | | 4.46 | 4.0 | 3.4 | 4.0 | 6.5 | 3.2 | | |
| | *n* | | 11 | 10 | 13 | 4 | 10 | 10 | 6 | 4 |
| dP4 | Average | x7x | 7.0 | 79.2 | 34.8 | 25.6 | 10.0 | 2.28 | | |
| Sup. | Min | | 7.0 | 79.2 | 34.5 | 24.1 | 9.7 | 2.28 | 2.0 | 65.0 |
| | Max | | 7.0 | 79.2 | 35.0 | 28.0 | 10.2 | 2.28 | 2.9 | 80.0 |
| | SD | | | | 0.2 | 2.1 | 0.3 | | | |
| | CV | | | | 0.6 | 8.9 | 2.7 | | | |
| | *n* | | 1 | 1 | 4 | 3 | 3 | 1 | 3 | 3 |
| dP4 | Average | x8x | 8.0 | 94.0 | 34.7 | 27.5 | 9.9 | 2.76 | | |
| Inf. | Min | | 8.0 | 94.0 | 34.0 | 26.4 | 9.5 | 2.76 | 2.2 | 72.0 |
| | Max | | 8.0 | 94.0 | 36.0 | 28.6 | 10.2 | 2.76 | 2.8 | 85.0 |
| | SD | | — | — | 1.1 | 1.6 | 0.5 | — | | |
| | CV | | — | — | 3.4 | 6.4 | 5.7 | — | | |
| | *n* | | 1 | 1 | 3 | 2 | 2 | 1 | | 4 |
| *M*1 | Average | −8x | 8+ | 77+ | 40.7 | 29.5 | 9.9 | — | | |
| Sup. | Min | | — | — | 40 | 28 | 9.3 | — | 1.7 | 67 |
| | Max | | — | — | 41.4 | 31 | 10.6 | — | 2.5 | 84 |
| | SD | | — | — | 0.99 | 2.12 | 0.67 | — | | |
| | CV | | — | — | 2.74 | 8.09 | 7.31 | — | | |
| | *n* | | 0 | 0 | 2 | 2 | 3 | 0 | 2 | 2 |
| *M*1 | Average | x8x | 8 | 102 | 35.3 | 27.8 | 8.8 | 2.89 | 1.6–2.6 | 76–79 |
| Inf. | *n* | | 1 | 1 | 1 | 1 | 1 | 1 | | |

Table 1 (*continued*)

| | | *P* | *P* | *L* | *W* | *H* | LF | *L*/*W* | ET | *h*/*w* |
|---|---|---|---|---|---|---|---|---|---|---|
| *M*2 | Average | x6– | — | 82+ | 50.0 | 42e | 7.0 | | 2.1–2.5 | 84–87 |
| Sup. | *n* | | 0 | 0 | 1 | 1 | 1 | | 1 | 1 |
| *M*2 | Average | x12x | 12 | 137 | 45.6 | 42 | 8.9 | 3.00 | 2.6–3.0 | 81–93 |
| Inf. | *n* | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *M*3 | Average | –9x | | 125+ | 59.4 | 50 | 6.3 | — | 2.9–3.4 | 83–88 |
| Sup. | *n* | | | | 1 | 1 | 1 | 0 | 1 | 1 |

For explanation of the parameters see appendix. Column 3 (plateformula P) indicates the variability in plate formulas of molars, where distinct plate formulas observed in various specimens of the same element are separated by dashes. In the $dP^2$ the plate formula "0" indicates that some specimens of this tooth do not have a single well-defined ridge.

plane (Maschenko, 2002). None of the *Stegodon* tushes occurs in a maxilla, but assuming homology with *Mammuthus*, the *Stegodon* tushes are compressed in medial–lateral direction. The medial–lateral diameter of the enamel crowns varies between 6.3 and 7.7 mm, the antero-posterior diameter between 7.4 and 10.0 mm. The height of the crown shows more variation, ranging between 9.5 and 15.0 mm. In none of the tushes could any signs of enamel wear be observed, suggesting that the tushes were non-functional. The enamel is less than 1 mm thick and thins out towards the root. Two weakly developed subparallel vertical grooves may be developed on the lateral face of the crown, running from the apex downwards and disappearing halfway down the crown. These grooves are reminiscent of the boundaries of the small enamel pillars or conules that are lengthwise attached to the lateral side of the crown in a milk tusk of *S. trigonocephalus* from Java (own observation). In lateral view the crown may show parallel margins, but more often these margins are bulging near the crown base. Weaker developed bulges are usually nearly symmetrical, but in a few specimens one of the bulges (anterior or posterior?) is more markedly developed than the opposite one (ICA no. 4.5.01-2: Plate 1, fig. 2a). In the latter specimen the entire root is preserved, measuring 45 mm. The total length of the milk tusk amounts to 55 mm. The root has a circular to oval cross-section. The lateral surface of the root is straight longitudinally, only bending slightly in medial direction towards the base. The medial side of the root is convex, with a maximum diameter of 9.4 mm in the middle, which is more than the horizontal diameter of the enamel crown (Plate 1, fig. 2b), like in *M. primigenius* (Maschenko, 2002). Delicate longitudinal grooves cover the root of the milk tusk. In two other specimens with the entire roots preserved (ICA no. 7.5.01-1 and 25.7.03-6), the outline in anterior view is weakly "S"-shaped, and the root has an oval cross-section. The total root length in these specimens is 50 and 52 mm, respectively. In all milk tusk roots the pulpa cavity is open.

In the African elephant the deciduous incisors are replaced after about 1 yr by a pair of continually growing permanent tusks (Sikes, 1971). This was also the case in *M. primigenius* (Maschenko, 2002). The individuals represented by the Liang Bua tushes thus probably died within 1 yr after their birth.

*$dP^2$*. $n = 11$ (four specimens occur in maxilla fragments; four are unworn). *Stegodon* dP2's are quite rare amongst fossil collections from Indonesia, and appear to be rather variable in morphology. Janensch and Dietrich (1916, Plate 3) figure a maxilla of *S. trigonocephalus* with an unworn $dP^2$ (by them identified as $P^2$) still in place. It has a subtriangular, rounded shape and bears three ridges. It was originally double rooted, but the posterior root had already been resorbed (Hooijer, 1955). Hooijer (1955) describes a maxilla of *S. trigonocephalus* from Java with both worn $dP^2$'s in place. Like the specimen described by Janensch and Dietrich, they have a subtriangular shape with three ridges and a double root. In an isolated $dP^2$ figured in the same paper, the three ridges are less well defined. Colbert and Hooijer (1953) mention that the $dP^2$ ($n = 7$) and $dP_2$ ($n = 4$) of *S. orientalis*, from the fissure fillings at Sichuan, China, bear three and two ridges, respectively. They do not give a detailed description, but from their table of measurements it follows that the $dP_2$ is considerably smaller than the $dP^2$. Hooijer (1955) further mentions that three juvenile *S. trigonocephalus* mandibles have a single alveolus with a circular cross-section of 9 mm. Thus the lower $dP_2$'s appear to be smaller and have fewer ridges as compared to upper $dP^2$'s. They have a single root, whereas the $dP^2$ is double-rooted.

Four *S.f. insularis* maxilla fragments from Liang Bua have the $dP^2$ in place. Three of these have a subtriangular rounded shape with two or three ridges and a double root. The anterior root points in anterolateral direction (Plate 1, fig. 10). The fourth specimen has an oval shape with transverse and antero-posterior diameters of 12.2 and 9.0 mm, respectively. This worn specimen differs from the others in having four well-defined pillars instead of ridges. A single worn conule on the buccal side is larger near its base than the three other worn conules (Plate 2, fig. 1b). Like the other specimens, it has a double root.

In addition, there are five isolated dP2's that, based on their subtriangular shape and relatively large size, most likely represent upper $dP^2$'s. These isolated specimens bear two or three, more or less well-defined ridges, with the tubercles not always neatly aligned (Plate 1, figs. 3–5).

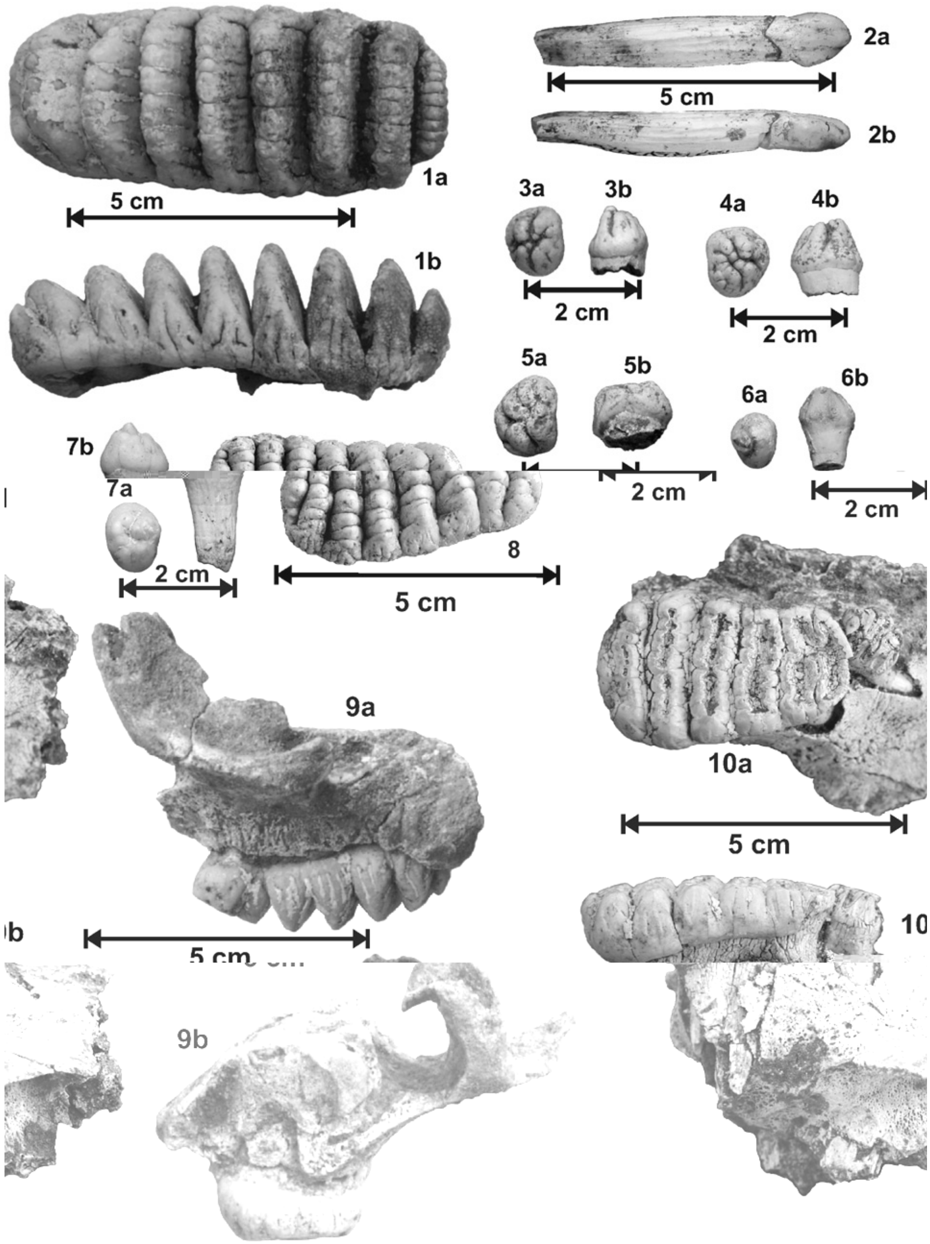


Plate 1. **Figs. 1–10.** *Stegodon florensis insularis* subspec. nov. **1.** ICA29.7.03-1: right $dP^4$; **1a.** occlusal view; **1b.** buccal view (real size). **2.** ICA4.5.01-2: right milktusk ($dI^2$); **2a**. lateral view; **2b.** posterior view (real size). **3.** ICA18.5.01-1: left $dP^2$; **3a.** occlusal view (anterior side to left); **3b.** buccal view (real size). **4.** ICA18.5.01-2: right $dP^2$; **4a.** occlusal view (anterior side to right); **4b.** anterior view (real size). **5.** ICA21.5.01-1: right $dP^2$; **5a.** occlusal view (anterior side to right); **5b.** posterior view (real size). **6.** ICA7.5.01-3: $dP_2$; **6a.** occlusal view; **6b.** posterior view (real size). **7.** ICA30.4.01-1: $dP_2$; **7a.** occlusal view (anterior side to right); **7b.** posterior view (real size). **8.** ICA320: left $dP_3$, occlusal view (real size). **9.** ICA10/5.7.03-1: left maxilla with $dP^3$; **9a.** lateral view; **9b.** anterior view (real size). **10.** ICA521: left maxilla with $dP^2$ and $dP^3$; **10a.** occlusal view; **10b.** lateral view (real size).

In all $dP^2$'s the transverse diameter is slightly larger than the antero-posterior diameter (average $W = 12.3$, average $L = 10.8$ mm). Specimen ICA 26.7.03-1 is the smallest $dP^2$. The enamel is slightly damaged on the buccal and lingual sides, but there are clearly three unworn ridges present. This is the only isolated $dP_2$ in which the double root is almost entirely preserved. It is 13 mm long, and splits in two diverging pulp canals near its base, one pointing in anterior and one in posterior direction.

*$dP_2$*. $n = 7$, (all isolated, of which four unworn). There are no juvenile mandibles with the $dP_2$ in place. A juvenile mandible fragment (ICA 503f) has the $dP_2$ alveolus represented by a single narrow, subrounded opening with a transverse diameter of 6 mm and an antero-posterior diameter of 7 mm. There are a number of isolated dP2's that have a single root and that have a suboval shape, contrary to the generally subtriangular shape of the $dP^2$. These are here attributed to lower $dP_2$'s. The $dP_2$'s of *S.f. insularis* are on average smaller than the $dP^2$'s, but likewise have a larger transverse diameter than antero-posterior diameter (average $W = 11.7$, average $L = 10.1$ mm). There are usually one or two, more or less defined ridges, but in

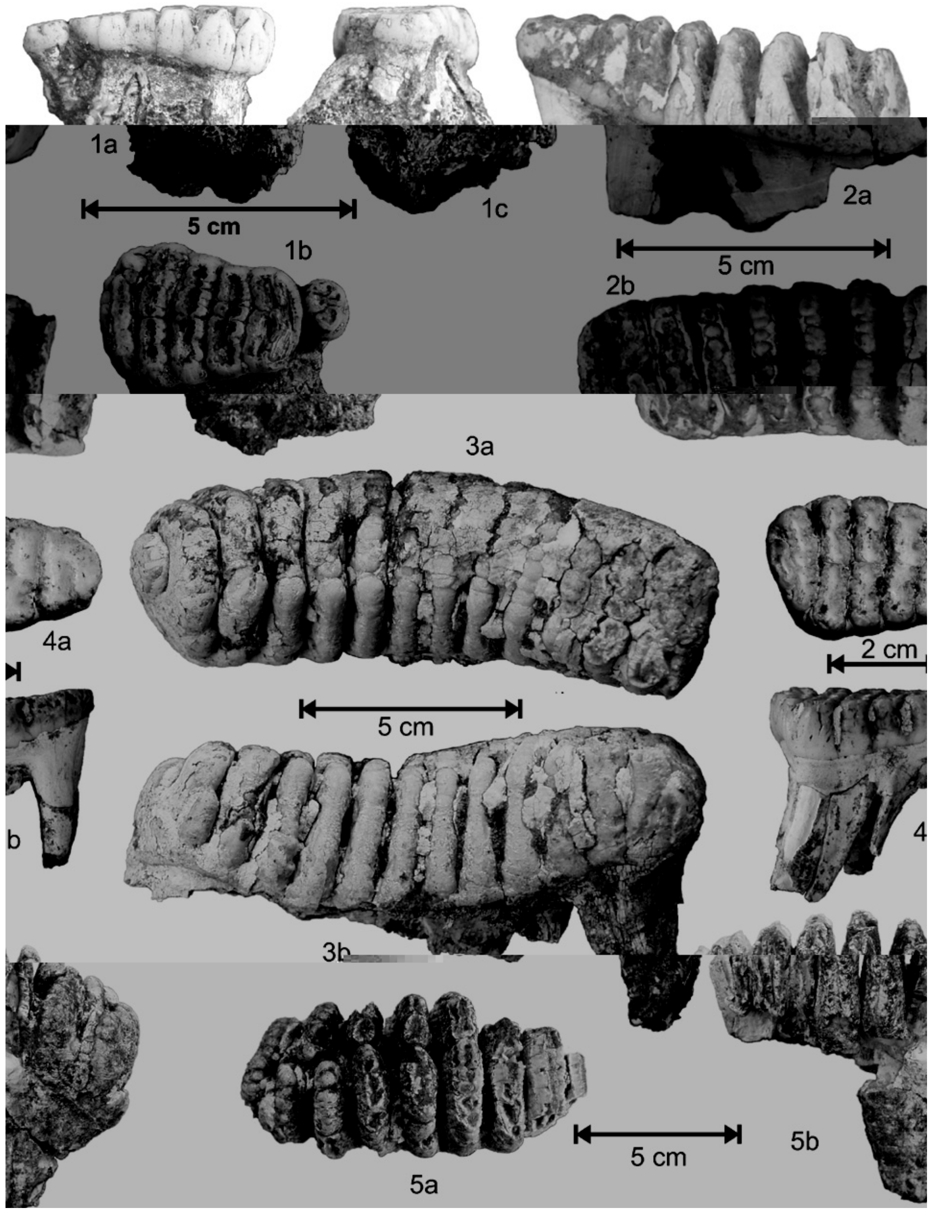


Plate 2. **Figs. 1–5.** *Stegodon florensis insularis* subspec. nov. **1.** ICA20.7.04R: left $dP^3 + dP^2$; **1a.** lingual view; **1b.** occlusal view; **1c.** anterior view (real size). **2.** ICA25.7.03-3: left $dP_4$ fragment; **2a.** buccal view; **2b.** occlusal view (real size). **3.** ICA456: right $M_2$, Holotype; **3a.** occlusal view; **3b.** buccal view (four-fifths of real size). **4.** ICA279b: right $dP_3$; **4a.** occlusal view; **4b.** buccal view (real size). **5.** ICA423: left $M^3$ posterior fragment; **5a.** occlusal view; **5b.** lingual view (three-fifths of real size).

the smallest specimen (ICA no. 7.5.01-3; Plate 2, fig. 6) the crown consists of a single conule. In this specimen, there is 7 mm of a single root preserved. The root is filled completely with dentine. In another specimen (ICA no. 30.4.01-1; Plate 1, fig. 7) the root is almost complete and 17 mm long, the pulpa cavity still open. In both specimens the root has a circular cross-section, tapers rapidly below the crown and then has a constant diameter over half its total length. Delicate longitudinal grooves are present along the posterior side, which is slightly concave. In specimen ICA 30.4.01-1 the crown has an oval cross-section and bears two ridges, the anterior ridge bearing two and the posterior ridge four weakly developed conules. One of the two anterior conules is larger than all others, but it is not clear whether this tubercle is located on the buccal or lingual side. The tips of the conules are polished by slight wear. In specimen ICA 8.7.03-2 the crown has seven small tubercles aligned in a half-circle that surrounds a single anterior tubercle, which is much wider and higher than the other tubercles. Furthermore, there are three poorly preserved dP2's that may represent either upper or lower ones.

*$dP^3$*. $n = 20$ (14 complete, of which seven in maxilla fragments and five unworn). Upper dP3's of *Stegodon* are relatively shorter and wider than their lower equivalents, as expressed by a smaller L/W index (in *S.f. insularis* between 1.38 and 1.63, versus 1.78 and 1.95 for lower $dP_3$'s). They also tend to have one ridge less than the lower counterpart.

The $dP^3$'s have a subrectangular shape with a constriction between the first and second ridges and a convex longitudinal wear surface (Plate 1, fig. 10; Plate 2, fig. 1). The $dP^3$'s from Liang Bua have five, but more often six fully developed ridges (on average 5.9 fully developed ridges). Specimens with five ridges have both an anterior and posterior half-ridge, whereas specimens with six fully developed ridges may have only an anterior or only a posterior half-ridge, or both. The $L$ varies between 40.0 and 49.3 mm ($n = 14$) and the W between 26.5 and 32.5 mm ($n = 20$).

With the exception of specimen ICA 28.7.03-6, all $dP_3$' have a well-developed median cleft in at least the anterior portion of the molar. This median cleft does not reach the crown base and upon increasing wear the buccal and lingual enamel wear figures coalesce into a single wear figure. Specimen ICA 28.7.03-6 is more rapidly widening in posterior direction as compared to the other specimens. Weak cementum may be deposited in the valleys between the ridges. The lamellar frequency (LF) varies between 12.2 and 14.3 ridges per 10 cm. The $h/w$ indices ($100 \times h/w$) of individual unworn ridges vary between 48 and 55. The number of conules per ridge is rather variable, the anterior ridges usually bearing only four, the wider posterior ridges up to 11 conules. The enamel, between 0.9 and 2.0 mm thick, is delicately folded.

*$dP_3$.* $n = 16$ (12 complete, of which four unworn, one in a mandible (Plate 3, fig. 4)). Two complete unworn specimens JR-8b and JR-15, and the fragments JR-9 and JR-12 have been used for combined ESR/U-series dating and could not be examined directly. They have been studied from photographs and their measurements have been estimated. The $dP_3$ has either six ridges with both an anterior and posterior half-ridge present, but more often seven ridges with either a posterior or an anterior half-ridge (on average there are 6.9 fully developed ridges). The general shape is subtrapezoidal, the maximum width usually occurring at the penultimate ridge, and an anterior constriction such as developed in upper $dP^3$'s is weaker developed (Plate 1, fig. 8) or lacking. Length varies between 45.4 and 51.4 mm ($n = 11$), and maximum width ($W$) varies between 24.5 and 28.5 mm; $n = 14$). The $h/w$ indices of individual, unworn ridges vary between 59 and 86. A median cleft is usually present, separating the buccal and lingual halves of the ridges halfway down their height, like in the upper $dP_3$'s (Plate 1, fig. 8; Plate 2, fig. 4). The LF varies between 12.5 and 15.1 ridges per 10 cm. The ET lies between 1.2 and 1.7 mm.

*$dP^4$.* $n = 4$ (one specimen is complete). The only complete unworn $dP^4$ (ICA no. 29.7.03-1; Plate 1, fig. 1) is of the right side and bears x7x ridges. In lateral view the base of the crown is convex in apical direction, clearly showing this milk molar to be an upper one. It has a subrectangular shape with an $L$ of 79.2 mm and a $W$ of 34.8 mm on the fifth ridge. This gives a $L/W$ ratio of 2.28, smaller than the lower equivalent. The buccal and lingual surfaces of the ridges have clear subvertical grooves developed, a character that is less strongly developed or absent in the last three molars of stegodonts. The conule tips of the unworn ridges form a convex transverse surface. The number of conules in individual ridges varies between four in the anterior and 11 in the posterior ridges. A weakly developed median cleft runs from the middle of the crown anteriorly to slightly buccally of the middle posteriorly. There are two small accessory conules closing the valley between the first and second ridge on the lingual and buccal side. Such additional conules are sometimes developed in *Stegodon* molars but have no taxonomic significance (Hooijer, 1955; van den Bergh, 1999). A very thin layer of cement covers the anterior two ridges only, leaving the conules free. The molar must have been largely inside the alveolus when the animal died.

For summary measurements of the single complete and three fragmentary $dP^4$ specimens see Table 1. The ET varies between 2.0 and 2.9 mm, thicker than in the $dP^3$ but overlapping with the $M^1$.

*$dP_4$.* $n = 5$ (one specimen is worn but complete, one with only the posterior half-ridge broken, and three smaller fragments. One dextral anterior fragment occurs in a juvenile mandible). The only complete lower $dP_4$ from Liang Bua is from the right side (specimen ICA 5/JR-14). It has been used for ESR/U-series dating and was examined from a photograph. It bears x8x ridges, all worn. The length can be estimated at 94e mm. An almost complete specimen (ICA no. 25.7.03-3; Plate 2, fig. 2) is of the left side and bears x8x ridges, with the posterior half-ridge damaged. The anterior five ridges are worn. The $L$ as far as preserved is 85.7+ mm and the $W$ amounts to 36 mm. Cement decreases in posterior direction, from a complete filling of the valleys to no cement at all on the last two ridges. A well-developed median cleft extends downwards to halfway the height of the ridges. The root is partly preserved in this specimen, the anterior root supporting x3 ridges. The ET varies to between 2.2 and 2.3 mm in this specimen, up to 2.8 mm when including the other fragmentary $dP_4$ specimens. The enamel is double layered, showing well-developed stepwise wear. The LF varies between 9.5 and 11.1 ($n = 3$).

Specimen ICA no. 28.7.03-8, of the right side, lacks an anterior and posterior portion. There remain -6- ridges, of which the anterior two are worn. This specimen is characterized by a very strongly developed median cleft, which extends down to the base of the ridges. The most posteriorly preserved ridge has a transverse width of 34.2 mm, which must be close to the maximum width. An anterior dextral $dP_4$ fragment occurs in situ in a mandible (ICA no. 672). It consists of x5- ridges, of which the anterior three are worn.

There remain a few fragmentary dP4 fragments, consisting of 3 or less preserved ridges. Based on the transverse diameters of their individual ridges, ET and the presence of subvertical grooves on the buccal and lingual sides of the ridges, these fragments can be determined as dP4's, either upper or lower ones.

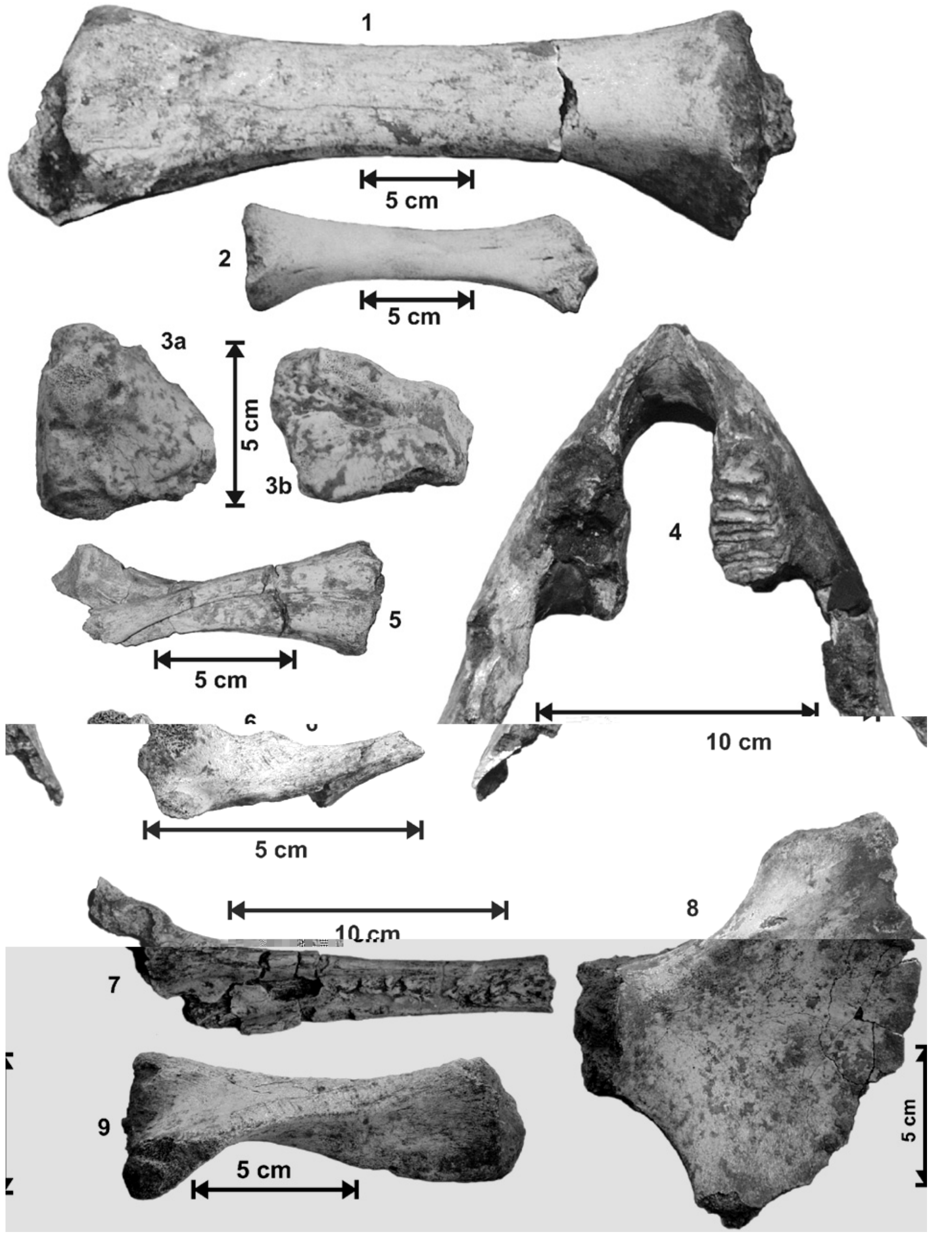


Plate 3. **Figs. 1–8.** *Stegodon florensis insularis* subspec. nov. **1.** ICA264: left femur diaphysis, subadult, anterior view (proximal side to the left; two-fifths of real size). **2.** ICA292: right femur diaphysis, neonate/juvenile, anterior view (proximal side to the right; two-fifths of real size). **3.** ICA26.7.03-2: right uncinatum; **3a.** proximal view; **3b.** medial view (three-fifths of real size). **4.** ICA671: mandible with right $dP_3$, occlusal view (half size). **5.** ICA287a: right ulna and radius diaphysis fragments (juvenile), posterior view (half size). **6.** ICA11.8.04: vertebra cervicale fragment, arcus fragment, cranial view (real size). Note the parallel cutmarks in the middle of the arch. **7.** ICA894A: vertebra thoracale fragment, dorsal spine (aged individual), caudal view (half size). **8.** ICA446a: left ilium fragment (juvenile), cranial view (half size). **9.** ICA517k: left humerus fragment (juvenile), caudal view (three-fifth of real size). Note the parallel rodent gnaw marks along the lateral epicondylar crest.

*$M^1$*. $n = 3$ (none complete). The most complete specimen (ICA no. 669 g) is a large posterior portion of a right $M^1$. The posterior five ridges plus a posterior half-ridge are intact but worn, save the last ridge. The 6th ridge from behind is more than half worn and is partly broken. The two ridges in front of it are worn down to the base and lack the buccal halves. The molar has -8x ridges, with a convex wear surface showing it to be an upper one. The *L* is 77+ mm. Partly broken cement is deposited in between the ridges and on the ridge flanks. The *W* amounts to 41.4 mm at the fifth ridge from behind. This is more than 6 mm wider than in the largest $dP^4$ (Table 1). The LF amounts to 9.7, which equals the lower limit of the LF range observed in the $dP^4$. The buccal and lingual sides of the ridges have only weakly developed subvertical grooves, unlike the $dP^4$, which has more marked and delicate grooves. The range of ET amongst the three specimens varies between 1.7 and 2.5 mm, overlapping with the range of the $dP^4$.

There's another right $M^1$ fragment from the same level in sector XI (ICA no. 669f). It is an anterior portion with x6- ridges preserved, of which the anterior two are slightly worn. In this specimen the unworn ridges were entirely covered with cement, including the conules and flanks. The width at ridge 5 amounts to 38.1 mm, which must be close to the maximum $W$ of the molar. The $h/w$ indices of individual unworn ridges vary between 76 and 84 in this specimen, and between 67 and 71 in the third $M^1$ specimen (ICA no. 449b), an unworn posterior fragment with -4x ridges is preserved.

$M_1$. $n = 1$ (complete). The only $M_1$ of *S.f. insularis* in the Liang Bua collection is of the right side (ICA no. VII-63; Plate 4, fig. 1). The total number of ridges is x8x, the same as in the only complete $dP_4$, but its $L$ is 102 mm, almost 1 cm longer than the $dP_4$. This gives a smaller LF of 8.8. The fact that the buccal and lingual sides of the ridges are rather smooth, and the relatively strongly developed cement further indicates that we are dealing with a $M_1$. Contrary to the $dP_4$, the difference in width between the anterior and the posterior ridge is not so marked in the $M_1$. The anterior six ridges are worn, with only the anterior two ridges showing fully developed wear figures. The maximum $W$ of 35.3 mm occurs at the penultimate ridge, which is within the $W$ range of the various $dP_4$ specimens (Table 1). However, the relatively small $W$ may be caused by a pathologic condition: the buccal side of the crown shows a marked concavity at the level of ridges 4–8.

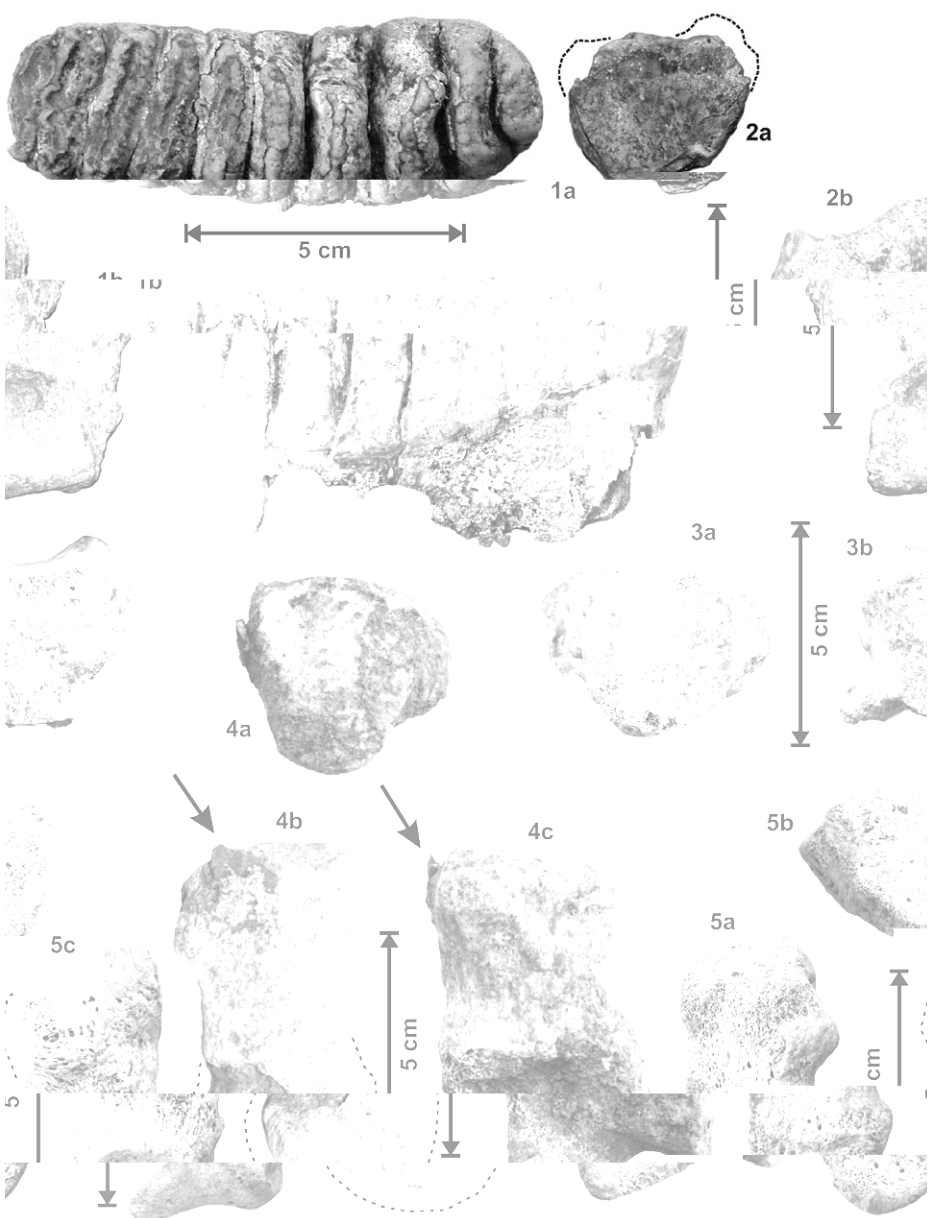


Plate 4. **Figs. 1–5.** *Stegodon florensis insularis* subspec. nov. **1.** ICA-VII-63: right $M_1$; **1a.** occlusal view; **1b.** buccal view (real size). **2.** ICA496a: right metacarpus V; **2a.** proximal view (medial side to left); **2b.** posterior (palmar) view (four-fifths of real size). **3.** ICA447b: left metacarpus V; **3a.** proximal view (medial side to left); **3b.** anterior (dorsal) view (four-fifths of real size). **4.** ICA25.7.03-7: left metacarpus IV; **4a.** proximal view; **4b.** lateral view; **4c.** posterior view (four-fifths of real size). **5.** ICA569: right metacarpus V; **5a.** medial view; **5b.** proximal view; **5c.** posterior view (four-fifths of real size).

This abnormality may have been caused by a mandibular abscess. There is no median cleft developed.

*$M^2$*. $n = 1$ (anterior fragment). The $M^2$ is represented by a single fragment (ICA no. 11.8.04-1) with x6- ridges preserved. The length of the specimen is 82+ mm as far as preserved. The anterior x2- ridges are damaged on the buccal side. The conules of the lingual side of the anterior ridge are abraded by wear, but the second ridge is not yet worn. There is one aberrant accessory conule developed on the buccal side in between ridges two and three. The crown base is concave towards the broken root, indicating an upper molar. Ridges five and six both have a width of 50 mm, which must be close to the maximum width ($W$). The ridges are inclined forward in lateral view and bear 6–8 conules of approximately equal size. The $h/w$ indices of unworn ridges vary between 84 and 87. The ET varies between 2.1 and 2.5 mm, overlapping with the ET of the $M^1$.

*$M_2$*. $n = 1$ (ICA no. 456, which is the complete type specimen). The type specimen is a dextral lower molar with x12x ridges (Plate 2, fig. 3). The root is largely broken, but a large portion of the anterior hook is preserved on the buccal side. The crown was originally covered with thick cement enclosing the conules and flanks, but the cement has been poorly preserved and is largely broken away along the buccal side of the tooth. The enamel of the anterior half-ridge and of the tips of the anterior two ridges is damaged. The conules of the third ridge are slightly abraded, but the dentine is not yet exposed. The type specimen is strongly concave longitudinally, both at the occlusal surface as well as along the buccal side. Contrary to the $M_1$, the maximum $W$ of the $M_2$ occurs halfway along the tooth at ridge 8 ($W$ is 45.6c mm, including ca. 0.5 mm of cement) and not at the posterior region of the tooth like in the $dP_4$ and $M_1$. In the $M_3$ of stegodonts the maximum $W$ occurs in the anterior part of the tooth, usually at the fifth ridge, whereas the ridges are gradually tapering in the posterior part. This is not the case in specimen ICA-456, and despite the large number of ridges, the morphology shows this specimen clearly to represent the penultimate molar, the $M_2$. The $L$ of the holotype specimen measures 137 mm. The $L/W$ ratio of the $M_2$ is 3.00, slightly larger than in the $M_1$, but the antero-posterior diameter of individual ridges at their base is comparable, as expressed by an LF of 8.9 (versus 8.8 in the $M_1$). Though the lamellar frequencies are similar, the ridges of the $M_2$ are clearly wider in transverse direction ($W = 45.6$c mm versus 35.3 mm in $M_1$). Also the enamel of the $M_2$ is thicker (ET varies between 2.6 and 3.0 mm) and comparatively less folded than in the lower rank molars. The roof-shaped ridges are very hypsodont, with $h/w$ indices of between 93 at the first unworn ridge (the third one), decreasing to 81 at the penultimate ridge. The number of conules per ridge is relatively low, with four in the anterior ridges to maximal eight conules in the posterior ones. No median cleft is developed. The enamel pattern of the (broken) occlusal surface of the second ridge shows a weak double median expansion, which is reminiscent of the median pillars encountered in the more primitive elephantoids.

*$M^3$*. $n = 1$ (posterior fragment). Specimen ICA no. 423 (Plate 2, fig. 5) is a large portion of sinistral $M^3$. The specimen is pathological in having a deep median cleft posteriorly, with an off-set between the buccal and lingual halves of the second–fourth ridges from behind along this cleft. The lingual portion of the penultimate ridge is not developed. Counted along the buccal side, the fragment bears seven ridges plus a posterior half-ridge. The medial remnants of two more half-worn ridges remain in front, giving a ridge formula of -9x. Preservation of the specimen is poor, with parts of the ridge bases broken. Cement has not been preserved except for some remnants in the valleys. Of the nine ridges the anterior five are worn. The enamel of the conules in the fourth ridge from behind is broken, so that it cannot be observed if they were originally abraded as well, but the conules of the third ridge from behind are unworn. The occlusal surface is convex. There are nine or ten conules developed in the fifth ridge from behind. The length, as far as preserved amounts to 125+ mm. The LF (measured on the fifth–seventh ridge from behind) amounts to 6.3, which is low compared to the LF of preceding molars of *S.f. insularis*, but high compared to the $M^3$ of larger sized stegodonts (e.g. ranging between 3.9 and 5.0 in the $M^3$ of *S.f. florensis* and between 3.3 and 5.0 in that of *S. trigonocephalus*). The width of the four worn ridges in front could not be measured because of damage of the ridge bases. The width at the fifth ridge from behind measures 59.4 mm, decreasing to 41e mm at the most posterior ridge. The posterior tapering and the relatively large $W$ of 59.4+ mm (ca. 10 mm more than the $W$ of the $M^2$), indicates that we are dealing with an $M^3$. The $h/w$ indices of the unworn third and fourth ridges from behind are 83 and 88e, respectively. The double-layered enamel has an ET of between 2.9 and 3.4 mm, which is again higher than in the preceding molar. The enamel is folded with 2–4 folds per cm and amplitude of 0.5–2.0 mm, less than the ET. The enamel surface of the lateral sides of the ridges is rough, lacking vertical grooves but showing well-developed perikymata.

### 5.2. Permanent tusks

There are 23 permanent tusk fragments in the Liang Bua collection, most consisting of very small fragments. Of only two fragments the diameter could be measured. One is a permanent tusk fragment of a juvenile individual (ICA no. 452b). The fragment has a poor, crumbly preservation and is only 22+ mm long as far as preserved. It has a weakly oval cross-section with a maximum diameter of 17.3 mm. The other specimen represents a proximal fragment of a tusk (ICA no. XI-35) preserved over a straight length of 280+ mm. The surface is weathered showing cracks and fissures. Proximally, the tip of the conical pulpa cavity is preserved. The maximum diameter at this end measures

77 mm. At the distal broken end the diameter amounts to 75 mm. The tusk fragment is weakly curved. Because of its relatively large diameter the fragment presumably belonged to an adult individual.

### 5.3. Mandible

There are two juvenile mandibles both originating from a single concentration level of bones and stone artefacts in sector XI, spit 48 (see Morwood et al., 2005: Supplementary Fig. A9). In addition, there are three juvenile mandible fragments amongst the fossil material. Specimen ICA-672 is the most complete mandible, with the symphysis and both horizontal ramii largely preserved. The milk molars from the left side have been lost. On both sides the alveoli of the $dP_2$'s have already disappeared, the most anterior alveoli present corresponding with the anterior hooks of the $dP_3$'s. On the right side the $dP_3$ is lost, but the anterior portion of the $dP_4$ is in place. The medial parts of both ascending ramii are broken away, and also both condyles are lacking. What remains is a large portion of both coronoid processes. The exposed alveoli in the ascending ramii are empty on both sides. Measurements of ICA no. 672 and another juvenile *S. trigonocephalus* mandible are given for comparison in Table 2.

The other juvenile mandible, ICA no. 671 (Plate 3, fig. 4), is of the same age class, but here the fully worn dextral $dP_3$ is present, whereas the $dP_4$ is missing from the alveolus. The anterior margin of the $dP_3$ has already been shed and like in the previous mandible the alveolus for the $dP_2$ has been resorbed. It also has the symphysis and both horizontal ramii largely preserved, but the ascending ramii are less complete than in the previous specimen. The maximum width of a single horizontal ramus (measurement 18 of van den Bergh, 1999) amounts to 51.5 mm in ICA no. 672 and 50e mm in ICA no. 671. Plotting these values in a graph of the mandible growth curves of other stegodont species (Fig. 3), it follows that the size of *S.f. insularis* plots in between the growth curves of *S.f. florensis* and *S. sondaari*, and would more or less correspond in size with that of *S. sompoensis* from Sulawesi (van den Bergh, 1999).

A third mandible fragment, ICA no. 503f, belonged to a still younger individual, possibly a neonate. It is a right horizontal ramus fragment lacking dentition. In front the fragment is broken at the symphysis, and at the rear the horizontal ramus is broken at the posterior part of the alveolus of the $dP_3$. In between the $dP_3$ alveolus and the interalveolar crest there is the alveolus of a $dP_2$, consisting of a single subrounded hole with a diameter of 6–7 mm. The minimum transverse diameter of the horizontal ramus in front of this alveolus (measurement 20 in van den Bergh, 1999) measures only 9 mm, versus 23 and 21 mm in specimens ICA-672 and ICA-671, respectively. On the remaining two juvenile mandible fragments no measurements could be taken.

Table 2
Size measurements of juvenile mandibles of *S.f. insularis* subsp. nov. and *Stegodon trigonocephalus ngandongensis* from the late Pleistocene of Java

| Measurement | *S. florensis insularis* | | | *S. trigonocephalus ngandongensis* |
|---|---|---|---|---|
| | ICA-671 | ICA-672 | ICA-503f | GRDC-K402 |
| *M*1 | 162+ | 170+ | — | — |
| *M*5 | 45 | 42+ | — | 75 |
| *M*6 | 43.5e | 38+ | — | 55 |
| *M*7 | 49 | 52 | 30 | — |
| *M*11 | 186+ | — | — | — |
| *M*15 | 140e | — | — | — |
| *M*16 | — | 174e | — | — |
| *M*17 | 35e | 41.5 | — | — |
| *M*18 | 52e | 51.5 | 33+ | 66 |
| *M*19 | — | 35 | — | — |
| *M*20 | 21.2 | 23 | 9 | 37 |
| *M*21 | 29+ | 42 | 22e | — |
| *M*22 | 44 | — | — | — |
| *M*24 | 51+ | 60e | — | 70e |
| *M*25 | 24.5 | 16.5+ | — | 30.5 |

For an explanation of the measurements see van den Bergh (1999). All mandibles are juvenile with the $dP_3$ in function. Specimen K402 represents a dextral mandibular ramus originating from Ngandong. It has a posterior $dP_3$ fragment in place with all ridges worn. In mandibles ICA-308 and 776, the $dP_2$ has been worn out and its alveolus already resorbed. ICA-503f and GRDC-K402 have a slightly younger dental wear age, because the root/alveolus of the $dP_2$ is not yet resorbed. $M1$ = maximum length; $M5$ = height of horizontal ramus measured at the level of the anterior border of the dental alveoles; $M6$ = height of horizontal ramus measured at the level of the anterior onset of the ascending ramus; $M7$ = length of the interalveolar crest; $M11$ = maximum width of the mandible measured between the external borders of the condyles; $M15$ = width of the mandible at the level of the onset of the ascending ramus; $M16$ = width of the mandible measured between the external borders of the coronoid apophyses; $M17$ = distance separating the internal borders of the horizontal ramii at the level of the onset of the ascending ramii; $M18$ = maximum transverse diameter of the horizontal ramus; $M19$ = distance separating the internal borders of the horizontal ramii at the level of the anterior border of the dental alveoli; $M20$ = minimum transverse diameter of the horizontal ramus (left or right); $M21$ = antero-posterior length of the symphysis; $M22$ = transverse distance between the superior terminations of the interalveolar crests; $M24$ = length of the occlusal wear surface (left or right); $M25$ = maximum width of the occlusal wear surface (left or right).

### 5.4. Cranium

There are no complete skulls preserved and generally skull parts are poorly preserved and fragmented. Isolated petrosum specimens are relatively common (12 specimens). A left squamosal of a juvenile individual (ICA no. 521d) includes the pars temporalis, the base of the broken processus zygomaticus of the squamosal, the meatus acusticus spurius and on the ventral side the fossa postglenoidalis. The superior rim of the pars temporalis is broken, but posteriorly the suture with the exoccipital is preserved as a rugose surface with grooves. In modern African elephants, the suture between squamosal and exocciptal closes during the ontogenetic stage when the

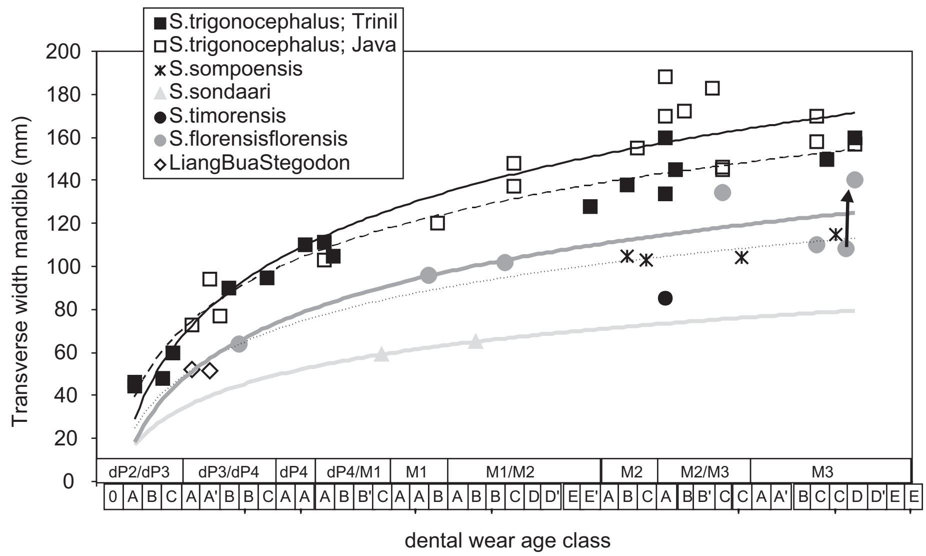


Fig. 3. Growth curve of the mandible plotted against dental wear age class for various Indonesian *Stegodon* species and subspecies. Plotted are the maximum widths of the horizontal ramus of the mandible as a function of dental wear age class (as defined for *Loxodonta africana* by Beden, 1979).

dP4's have been shed, indicating that specimen ICA-541d belonged to a juvenile individual. In cross-section the bone of the pars temporalis has well-developed air cells, which in mammoths and modern elephants develop during the first 3 yr of growth (Sikes, 1971; Maschenko, 2002). Their presence indicates that specimen ICA-521d was not a neonate. The distance between the anterior edge and posterior suture with the exoccipital measures 98 + mm. On the medial side the internal surface of the brain cavity is exposed, which measures 67 + mm in antero-posterior direction. The dorsoventral diameter of the external ear opening is 17.7 mm, and 21.0 mm in antero-posterior direction.

Two parietal fragments of juvenile individuals originate from the same bone concentration in sector XI. Specimen ICA-521b is a left parietal fragment. The sutures with the opposite parietal and the occipital are largely preserved, but the anterior and lateral borders are broken. The posterior area of the parietal is only weakly convex in antero-posterior direction, but bends down in a rounded curve about halfway along the median suture. The fragment measures 75 + mm in longitudinal direction. The bone is 5 mm thick along the medial suture at the most anterior preserved portion, and thickens in posterior direction to 14 mm near the suture with the occipital. The suture shows faint curved grooves perpendicular to the outer and inner surface of the parietal. The surface of the suture consist of spongiose bone, but the large air cavities characteristic for proboscidean skull bones are not yet developed, showing this individual to be in an early postnatal stage. In transverse direction the parietal is more convex than in antero-posterior direction, the plane of the most lateral portion making an angle of 45° with the medial plane. The transverse width measured parallel to the horizontal plane amounts to 84 + mm. Thus, the brain case must have been at least two times as wide, more than 168 + mm. The concave inner surface of the parietal shows a faint imprint of the brain convolutions.

The other parietal fragment (ICA no. 521c) is likewise from the left side, but belonged to a slightly older individual in which the bone was thicker. The thickness of the parietal along the median suture amounts to 7.5 mm anteriorly and 24 mm posteriorly, more than in the previous specimen. The medial suture is eroded and does not show the suture grooves visible in the previous specimen, but likewise the bone is spongeous lacking the large air cavities seen in adult skulls. The posterior suture with the occipital shows delicate vertical grooves, again developed in spongiose bone with elongate cells. The length as far as preserved is 86 + mm, the width 64 + mm. In transverse direction the outer surface is weakly convex, but does not show the strong downward curvature seen in the previous specimen, because the lateral edge of specimen ICA-521c is broken closer to the median suture, preserving only the parietal protuberance.

A juvenile maxilla fragment with the partially worn $dP^3$ in place (ICA no. 10/5.7.03-1; Plate 1, fig. 9) has the inferior border of the orbital and the processus palatinus of the maxilla preserved. The horizontal diameter from the processus lacrymalis to the suture with the processus frontalis of the jugale measures 38.5 mm. The horizontal distance between the suture of the palate and the exterior margin of the orbital border, which is half the maximum width of the cranium, measures 77 mm. This gives a total width of the skull of ca. 154 mm. In the skull of an ontogenetically slightly older *S. trigonocephalus* individual from the locality Ngrawan on Java (Geological Research and Development Centre in Bandung—GRDC no. 131), the $dP^3$ is fully worn and the first ridge of the $dP^4$ is just abraded. In this skull the maximum skull width can be estimated at 366e mm, more than twice as large.

In specimen ICA-10/5.7.03-1 the infraorbital foramen is relatively large, with a diameter of 14.8 mm.

In another less complete juvenile maxilla fragment of an individual in which none of the ridges of the $dP^3$ are worn (ICA no. 25.7.03-2), the diameter of the infraorbital foramen is 11.1 mm. The horizontal diameter from the processus lacrymalis to the broken margin of the inferior border of the orbit is 57.6 + mm (65e mm), smaller than in specimen ICA no. 10/5.7.03-1.

### 5.5. *Postcranial skeleton*

Most of the postcranial elements of *S.f. insularis* belonged to juvenile individuals with the epiphyses unfused and lacking. Of the 45 identifiable postcranial parts only 12 specimens (26.7 per cent) belonged to mature individuals with fully fused epiphyses, allowing for metrical comparison with homologue elements of adult *S.f. florensis* and other elephantoids. Descriptions and comparisons of postcranials are given in the appendix. Size comparisons of the few postcranial elements of which one or more full-grown specimens of both *S. florensis* subspecies are available (thoracic vertebrae, uncinatum, metacarpus IV, metatarsal IV) show a linear size reduction of between 1.8 and 29.5 per cent.

## 6. Variation of dental elements

All dental elements of the Liang Bua stegodont are represented by at least one fragmentary molar, except the lower $M_3$. The available material shows that the upper and lower molar series are morphologically and biometrically uniform (Fig. 4; Table 1). For instance, in the dP3's, which is the most frequently encountered element, the Coefficient of Variation (CV) of various parameters varies between 3.2 and 7.5, which is comparable to variation in samples representing living populations of elephants or fossil tooth samples originating from single localities (Roth, 1992). Variation in the Liang Bua dP2 samples is much larger (CV varies between 9.4 and 15.4; for the number of ridges even 47.4), but the highly variable first milk molar also shows larger CV's in living populations (Roth, 1992). Based on the dental elements it can thus be concluded that the Late Pleistocene deposits at Liang Bua contain the remains of a single *Stegodon* (sub)species. The Liang Bua *Stegodon* molars are on average 30 per cent smaller in linear dimensions as compared to molars of *S. florensis* (Table 4) from the Soa Basin, though the largest dental and full-grown postcranial elements from Liang Bua reach the lower size limits observed in homologue elements from the Soa Basin. Given the typical sexual size dimorphism of elephants, it seems likely that the males of the Liang Bua stegodont could reach a comparable size as the females of *S. florensis* from the Soa Basin.

## 7. Relationship

The family Stegodontidae has its origin in the Early Miocene of Asia and is composed of two genera, *Stegolophodon* and *Stegodon*. The genus *Stegodon* remained largely restricted to Asia, but thrived there throughout the Plio-Pleistocene, with a centre of radiation located in Southern China (Saegusa, 1996, 2001). Based on cladistic analysis of skull characteristics Saegusa (1987, 1996) proposed that seven species of *Stegodon* (*S. zdanskyi*, *S. aurorae*, *S. trigonocephalus*, *S. ganesa*, *S. bombifrons*, *S. insignis* and *Stegodon* spec. A) should be allocated in a monophyletic subgroup, *Stegodon sensu stricto* (*s.s.*). The morphology of a juvenile *S. florensis* skull from the 850 ka-old locality Kopo Watu on Flores indicates that *S. florensis* can be added to the *Stegodon s.s* subgroup (van den Bergh et al., 2001b). It differs from most of the other species in this subgroup by the relatively narrow and hypsodont molars, a character that evolved independently in an other island stegodont from the *Stegodon s.s.* subgroup, namely *S. aurorae* from Japan.

Unlike the Elephantidae, the Stegodontidae are known to have been rather conservative in tooth morphology, the

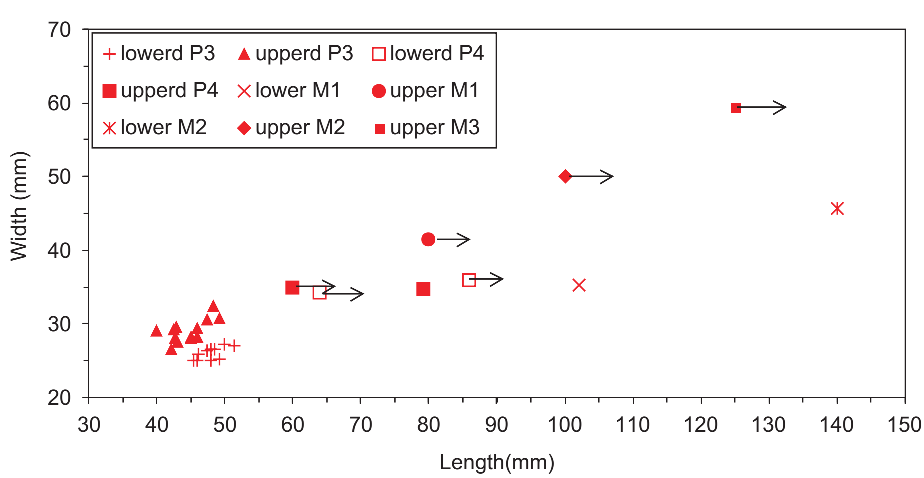


Fig. 4. Scatter diagram of the *Stegodon florensis insularis* molars from Liang Bua. Incomplete molars of which only the maximum width could be measured are indicated with arrows, indicating that the length is larger than the values shown by the symbols.

single most obvious trend being an increase in the number of ridges, in particular in the last three molars. This conservatism in molar morphology hampers classification based on molar morphology alone (Saegusa, 1987, 1996). Still, because the lack of significant adult skull and postcranial material, the molar morphology offers at present the only footing, besides body size, for taxonomic classification of the Liang Bua *Stegodon*.

On the basis of dental characteristics, chronology and geography, the Liang Bua stegodont is most likely a direct descendant of *S. florensis*. The Liang Bua stegodont is here classified as a new subspecies: *S. florensis insularis* subspec. nov. The ancestral *S. florensis* from the Soa Basin should then be designated as *S.f. florensis*. The Soa Basin and Liang Bua stegodonts are considered as two chrono-subspecies.

Proof for the presence of *S.f. florensis* on the island ranges between 850 and 700 ka, but so far no deposits with ages intermediate between those of the Soa Basin and of the Liang Bua sequence have yielded relevant fossil remains.

The fossiliferous deposits and the age structure of the fossil assemblage of the stratigraphic still older *S. sondaari* from the single locality Tangi Talo, show evidence for mass death associated with a volcanic event (van den Bergh, 1999). No remains attributable to *S. sondaari* were found higher up in the sequence, suggesting that a massive volcanic eruption led to the extinction of *S. sondaari*. The species possessed some primitive features, such as molar enamel with a weakly developed 3D inner enamel layer, relatively broad molars, and less molar ridges per homologue molar as compared to *S. florensis* and the Liang Bua stegodont (Table 3). *S. sondaari* is the smallest stegodont so far recorded. After its extinction around 900 ka, a new immigration of the more advanced, large to intermediate-sized *S.f. florensis* occurred (van den Bergh, 1999). In the various localities that yielded *S.f. florensis* remains (Morwood et al., 1998; van den Bergh, 1999; O'Sullivan et al., 2001), there are no indications for catastrophic mass-death events.

In a recent paper by Jacob et al. (2006), the evidence for multiple stegodont migrations to Flores is used as an argument against genetic isolation and allopatric speciation of *H. floresiensis*. However, this notion completely misses the point that in order to reach the island of Flores, both stegodonts and hominins had to cross one of the most prominent zoogeographic boundaries that has been distinguished: Wallace's Line (van Oosterzee, 1997). There is ample evidence that members of the proboscideans have a high potential to cross water barriers swimming (Sondaar, 1977; Johnson, 1978), reaching as far East as Sulawesi, Sumba and even Timor. More than other groups of

Table 3
Ridge-crest formulas of *Stegodon florensis insularis* subsp. nov. from Liang Bua as compared to various other *Stegodon* (sub)species

| | | dP2 | dP3 | dP4 | *M*1 | *M*2 | *M*3 |
|---|---|---|---|---|---|---|---|
| *S. elephantoides* | Upper | — | — | — | 6 | 6 | — |
| | Lower | — | — | — | — | — | 10 |
| *S. sondaari* | Upper | — | 6–7 | 6 | 6–7 | — | 8 |
| | Lower | — | 6 | — | 8 | 8 | 8 |
| *S.florensis florensis* | Upper | — | — | 6 | 7 | — | 12 |
| | Lower | — | — | 7–8 | 8–9 | 10 | 13–14 |
| *S. florensis insularis* | Upper | 0–3 | 5–6 | 7 | 8+ | — | 9+ |
| | Lower | 1–2 | 6–7 | 8 | 8 | 12 | — |
| *S. trigonocephalus praecursor* | Upper | — | — | — | — | — | — |
| | Lower | — | — | — | — | — | 11 |
| *S. trigonocephalus trigonocephalus* | Upper | — | 6 | 7–8 | 7 | 9 | 11 |
| | Lower | — | 6 | 8 | 8–9 | 10 | 13 |
| *S. trigonocephalus ngandongensis* | Upper | — | — | — | — | — | — |
| | Lower | — | 7 | 9 | 9+ | — | — |
| *S. zdanski* | Upper | — | 4 | 5 | 5 | 5–6 | 6–7 |
| | Lower | — | 4 | 6 | 5 | 6 | 7–8 |
| *S. orientalis* | Upper | 3 | 5–6 | 6–7 | 6–7 | 6–8 | 11–12 |
| | Lower | 2 | 5–6 | 7 | 7–8 | 7–9 | 12 |
| *S. sompoensis* | Upper | — | — | 7 | — | 8 | 8–9 |
| | Lower | — | — | — | — | 8 | 9–10 |
| *S. insignis* | Upper | 2 | 5–6 | 7 | 7–8 | 7–8 | 10–11 |
| | Lower | 2 | 6 | 7–9 | 7–10 | 9 | 11–13 |

Data updated from van den Bergh (1999).

terrestrial mammals, members of the proboscideans were able to cross Wallace's Line several times swimming (van den Bergh et al., 2001a). Their excellent swimming capacities are likely related to an aquatic ancestry (Gaeth et al., 1999). It is much harder to imagine that primitive hominins without proper boat technology could have crossed multiple times the sea straits between Bali and Lombok and between Sumbawa and Komodo intentionally. Even during periods of low sea level, these narrow straits acted as passages through which seawater flowed from the Pacific to the Indian Ocean Basins. The strong currents passing through these gaps prevented other mammals such as suids, cervids or bovids from crossing over to Flores throughout the Pleistocene. We speculate that it was probably easier to reach Flores overseas from the North (from Sulawesi/Selayar) using the prevailing southerly currents.

Early Pleistocene sea crossings by hominins were likely random events, e.g., as a result of natural disasters such as tsunamis, which occur frequently in this tectonically active region. The Indian Ocean tsunami that struck the coast of Aceh on December 26, 2004, has proven that humans who cannot swim and were dragged into the sea by a tsunami can survive for several days on natural rafts, floating large distances with the surface currents (http://news.bbc.co.uk/2/hi/asia-pacific/4151059.stm). A pregnant woman who could not swim was saved after 5 days from a sago tree and another man clinging to a tree was saved 160 km from the coast following 8 days at sea. Over a period of hundred thousands of years, the chances of a small group of hominins reaching Flores unwillingly in such a way must be taken into consideration.

*S.f. insularis* and *S.f. florensis* share a number of dental characteristics. They both possess relatively narrow teeth ($L/W$ amounts to 2.8 in $dP^4$ specimen ICA-29.7.03-1 compared to 2.11+ in *S.f. florensis* ($n = 1$)). These $L/W$ indices are larger as compared to the *S. trigonocephalus* lineage from Java, and to *S. sompoensis* known from the Early Pleistocene of Sulawesi. In *S. trigonocephalus* the $L/W$ index of the $dP^4$ varies between 1.9 and 1.96 ($n = 6$) and in *S. sompoensis* it amounts to 1.91 ($n = 1$). Also, *S. sondaari* possesses relatively broader molars than *S. florensis*, with the $L/W$ index of the $dP^4$ ranging between 1.88e and 2.11 ($n = 4$). The other *S. florensis* molars are also relatively narrow. Furthermore, both *S.f. insularis* and *S.f. florensis* share the possession of very hypsodont molars (compare Tables 1 and 4) as compared to *S. trigonocephalus* from Java. However, a relatively high hypsodonty is shared with other endemic island stegodonts such as *S. sondaari* and *S. sompoensis*, and may have resulted from parallel evolution as an adaptation to the consumption of tougher food contaminated with grit, such as grasses (van den Bergh, 1999).

During some 600 kyr of evolutionary adaptation to the island environment, changes included size reduction and an increase in the number of molar ridges: the $dP^4$ and $M^1$ of *S.f. insularis* have one additional ridge while the $M_2$ has two additional ridges as compared to *S.f. florensis*. The increase in the number of molar ridges is thought to have been an adaptation to more erosive food types on Flores and the need to increase masticatory efficiency, such as also occurred in other elephantoid lineages like *Mammuthus* and *Elephas*.

In Java we see a similar trend of increasing amount of molar ridges through time as recorded in three successive evolutionary stages of *S. trigonocephalus* that can be classified as chrono-subspecies, from old to young: *S. t. praecursor, S. t. trigonocephalus* and *S. t. ngandongensis* (van den Bergh, 1999; Table 3). However, because Java was intermittently connected to the Asian mainland, as expressed by the associated continental fossil faunas, drastic size reduction of *S. trigonocephalus* through time did not take place. But on Flores, not connected by intermittent land bridges even during periods of low sea level, the *S. florensis* lineage dwarfed. Other dwarfed elephantoids are known from islands off the coast of California, Southeast Asia and the Mediterranean (e.g. Roth, 1990, 2001; Mol et al., 1996; van den Bergh et al., 1996; Palombo, 2005).

Various factors have been proposed to explain dwarfing of large herbivores on islands (e.g. Foster, 1964; Sondaar, 1977; Case, 1978; Lomolino, 1985; Roth, 1990; Raia et al., 2003; Palombo, 2006). Dwarfing is either seen as a response to limited resources, the lack of top-order mammalian carnivores, the demographic advantages of having an accelerated reproduction and shortened gestation period in "risky" island environments, and in the tropics perhaps more effective thermo-regulation, or a combination of various factors. Raia and Meiri (2006) presented strong evidence that the most important factor for dwarfing of large ungulates on islands consists of the absence or reduced competition from other herbivores, and to a lesser extent absence of predators. A major advantage of having large body size, the ability to travel large distances in search for water and food resources is of limited use on islands like Flores.

The *Stegodon* sequence on Flores illustrates both the risks inherent in living on an island and the process of endemic dwarfing. On the island there are now two *Stegodon* colonisation–dwarfing–extinction cycles known. *S. sondaari* from the 900 ka-old site of Tangi Talo in the Soa Basin is the smallest recorded stegodont species. It resulted from endemic dwarfing on Flores from an as-yet unknown ancestor, possibly *S. elephantoides*, which has been recorded from Myanmar and a 1.2 Ma-old site on Java (van den Bergh, 1999). Following the extinction of *S. sondaari* around 900 ka, by 850 ka Flores was recolonized by *S.f. florensis*, which arrived either from Java in the west via the stepping stone islands Lombok and Sumbawa, or, alternatively from Sulawesi in The North. The poorly known *Stegodon* species B from the Middle Pleistocene Tanrung Formation in South Sulawesi (van den Bergh, 1999) could be closely related to *S. florensis*. After arrival on Flores it was then subject to the same process of

Table 4
Summary measurements of *Stegodon florensis florensis* molars from the Soa Basin, Flores

| | | *P* | *P* | *L* | *W* | *H* | *LF* | *L*/*W* | ET | *h*/*w* |
|---|---|---|---|---|---|---|---|---|---|---|
| dP3 | Range | | 3– | — | 34 | — | 12.5e | — | 1.0–1.1 | — |
| inf. | *N* | | 0 | 0 | 1 | 0 | 1 | 0 | | |
| dP4 | Average | x6x | 6 | 94+ | 44.6c | — | 8.4 | 2.12+ | 2.2 | — |
| Sup. | *n* | | 1 | 0 | 1 | 0 | 1 | 0 | | |
| dP4 | Average | (1)7x/x7x | 7.5 | 92 | 42.1 | 32.5 | 8.5 | 2.33 | 2.2–2.5 | 79 |
| Inf | Min | | 7 | 92 | 39.5 | 31.0 | 8.5 | 2.33 | 2.2 | 77 |
| | Max | | 8 | 92 | 44.0 | 34.0 | 8.5 | 2.33 | 2.5 | 91 |
| | SD | | — | — | 2.25 | — | — | — | | |
| | CV | | — | — | 5.67 | — | — | — | | |
| | *n* | | 2 | 1 | 4 | 2 | 1 | 1 | | |
| *M*1 | Average | x7x | 7.0 | 126.0 | 57.1 | 38.3 | 6.7 | 2.25 | | |
| Sup. | Min | | 7 | 125.0 | 53.5 | 38.3 | 6.1 | 2.16 | 3.3 | 56 |
| | Max | | 7 | 126.9 | 59.7 | 38.3 | 7.2 | 2.39 | 4.1 | 72 |
| | SD | | — | 0.95 | 2.62 | — | 0.50 | 0.12 | | |
| | CV | | — | 0.82 | 4.87 | — | 7.96 | 5.81 | | |
| | *n* | | 2 | 3 | 4 | 1 | 4 | 3 | | |
| *M*1 | Average | x8x/x9x | 8.5 | 142.7 | 55.0 | 37.5 | 6.2 | 2.65 | | |
| Inf | Min | | 8 | 134 | 53.8 | 37 | 6.0 | 2.54 | 3.0 | 65.1 |
| | Max | | 9 | 147.9 | 56 | 38 | 6.51 | 2.73 | 3.8 | 77 |
| | SD | | 0.58 | 6.37 | 0.93 | — | 0.21 | 0.10 | | |
| | CV | | 7.22 | 4.74 | 1.80 | — | 3.46 | 3.98 | | |
| | *n* | | 4 | 4 | 4 | 2 | 5 | 3 | | |
| *M*2 | Average | $-\frac{1}{2}$ 6x- | — | 150e | 61.6 | 47.2 | 5.75 | 2.43 | | |
| Sup. | Min | | — | 150.0 | 61.6 | 47.2 | 5.1 | 2.43 | 3.1 | |
| | Max | | — | 150.0 | 61.6 | 47.2 | 6.4 | 2.43 | 5.4 | |
| | *n* | | 0 | 1 | 1 | 1 | 2 | 1 | | |
| *M*2 | Average | x10x | 10 | 187.0 | 63.55 | 44 | 5.28 | 3.10 | | |
| inf. | Min | | 10 | 187.0 | 60.4 | 44 | 4.66 | 3.10 | 3 | 71 |
| | Max | | 10 | 187.0 | 66.7 | 44 | 5.9 | 3.10 | 3 | 75 |
| | *n* | | 1 | 1 | 2 | 1 | 2 | 1 | | |
| *M*3 | Average | x12x | 12 | 255 | 79.1 | 59 | 4.9 | 3.06 | | |
| Sup. | Min | | 12 | 240 | 67.0 | 56 | 3.85 | 2.93 | 3.2 | 60 |
| | Max | | 12 | 270 | 86.8 | 62 | 5.9 | 3.18 | 5.7 | 83 |
| | SD | | — | — | 6.45 | — | 0.51 | — | | |
| | CV | | — | — | 8.36 | — | 10.51 | — | | |
| | *n* | | 2 | 2 | 10 | 2 | 18 | 2 | | |
| *M*3 | Average | x13x/x14x | 13.5 | 291.0 | 71.4 | 53.7 | 5.0 | 3.77 | | |
| inf. | Min | | 13 | 282.0 | 59.4 | 48.5 | 4.6 | 3.69 | 2.9 | 67.1 |
| | Max | | 14 | 300.0 | 78.0 | 57.0 | 5.5 | 3.85 | 5.9 | 81 |
| | SD | | — | — | 5.59 | 4.12 | 0.32 | — | | |
| | CV | | — | — | 8.05 | 8.05 | 6.55 | — | | |
| | *n* | | 2 | 2 | 9 | 5 | 11 | 2 | | |

endemic dwarfing, culminating during the Late Pleistocene in *S.f. insularis*. During the relatively short time span that is covered by the excavated Liang Bua sequence, a period of roughly 80,000 yr, there is no indication for gradual size reduction. For instance, both the largest and the smallest $dP_3$ of the entire assemblage occur in the same spit (sector XI, spit 46).

On Flores the *S. florensis* lineage underwent considerable size reduction despite the presence of large reptilian predators, *V. komodoensis* and crocodiles, and possibly also a mammalian predator, *H. floresiensis*. The presence of stone artefacts at various Early to early Middle Pleistocene sites in the Soa Basin in association with *S.f. florensis* fossils proves that hominins were present, though no associated hominin remains have been discovered so far (Morwood et al., 1997; Brumm et al., 2006). Neither is there any proof for the notion that these hominins actively hunted stegodonts, at least not initially during the Middle Pleistocene. The absence of other large-sized herbivores on Flores would be conform the observations provided by Raia and Meiri (2006) that dwarfing of large ungulates on islands depends primarily on the absence of other large or medium-sized herbivores and the availability of empty niches. Lack of competition from other large herbivores on

Flores led to a linear size reduction of more than 30 per cent as compared to the colonizing stegodont population, while the co-occurrence of large predatory animals may have prevented *S. florensis* from reaching minimal size associated with an optimal energetic balance, in a similar way as advocated by Palombo (2006) for several well-documented Mediterranean endemic island faunas containing proboscideans.

Over a period of at least 600,000 yr both stegodonts and hominins could have dwarfed simultaneously in a co-evolutionary adaptation to the island environment. Fossil finds from new intermediate-aged sites on Flores could help illuminating the evolutionary mechanisms and rates responsible for dwarfing.

## 8. Age structure

Because of the unusual way of horizontal tooth replacement in stegodonts, which is shared with elephants, it is possible to give a fairly accurate estimate of the composition of the death assemblage from a certain site, based on isolated dental remains. Besides, the individuals can relatively easily be grouped into age classes based on the dental wear stages. The age structure from such a locality can tell us in some cases whether the mortality was selective or non-selective. In case of non-selective mortality, e.g. due to a catastrophic event that affected individuals of all ages to the same degree, the age structure of the death assemblage should correspond to the age structure of the living population. If selective mortality has occurred, e.g. due to predation, then certain age classes are over-represented. In case of predation there will be a disproportional large amount of juvenile and senile individuals (Haynes, 1991).

In Liang Bua assemblage it is relatively easy to attribute the molar remains to a MNI by direct comparison and fitting. Certain elements could be assigned to a single individual with certainty, like the left and right upper dP$^{3}$'s ICA-655 and ICA-656, both from sector XI spit 49. In other cases, two or more elements of different rank and representing upper and lower elements, were counted as a single individual if they showed the same dental wear age class, e.g. a fully worn left dP$_{3}$ and a right dP$^{4}$ of which only the first two ridges are worn, and provided that they were not found separated more than 30 cm in the vertical column (30 cm is the approximate depth of desiccation cracks observed in the cave during the dry season, and vertical displacement over such a distance may have occurred). For the assignment of dentitions to dental wear age classes, the classification of Beden (1979) was used as described in van den Bergh (1999). The advantage of this method is that Beden's classification is based on dentitions of *Loxodonta africana*, which has approximately equivalent numbers of ridges or molar plates in homologue molars as compared to *Stegodon*. The classification system has 43 dental wear age classes, from neonate individuals (dP2 and dP3 lacking any wear) to senile (M3 fully worn down to the rootmass).

With this method, the MNI was calculated at 47 individuals. The age structure of this composite death assemblage, which spans a time period of around 80,000 yr, is strongly dominated by juveniles (Fig. 5). Of the 47 individuals recognized, 94 per cent were juveniles, and 23 per cent of the MNI even represented neonate individuals. Of the 45 postcranial elements there were 11 specimens (24.2 per cent) with fused epiphyses, also suggesting a strong dominance of juvenile individuals. The extremely high proportion of juvenile individuals is much higher than the juvenile abundance of *Elephas falconeri* individuals from Spinagallo Cave on Sicily, which amounted to 59 per cent of the total assemblage (Raia et al., 2003). The extremely high abundance of *S.f. insularis* juveniles clearly indicates selective mortality. Such an age profile may be resulting from predation or (periodic) drought/food shortage, primarily affecting the juveniles (Haynes, 1991), or selective entrapment of

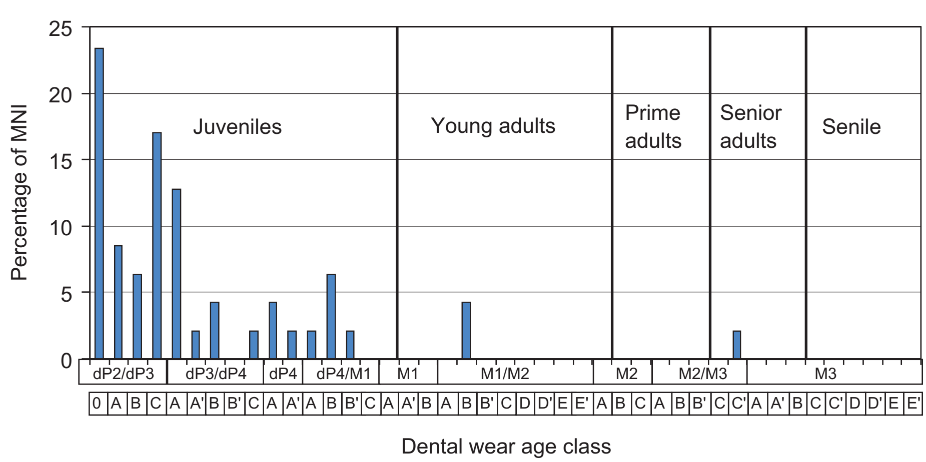


Fig. 5. Time-averaged dental wear age profile of the Liang Bua *Stegodon* molar assemblage. The 43 dental wear age classes on the horizontal axis are based on the work of Beden (1979). The vertical lines separate the five age groups of approximately equal life span (each equivalent with 12 African Elephant Years) distinguished by Haynes (1991; see also van den Bergh, 1999).

unexperienced juveniles in slippery pools of standing water or fissures.

A Middle Pleistocene *Stegodon orientalis* assemblage from Panxian Dadong cave in South China, shows similarity with Liang Bua in a number of characteristics. This assemblage is likewise dominated by primarily dental remains of juvenile individuals, and is associated with stone artefacts and human remains (Schepartz et al., 2005). This *Stegodon* assemblage has been interpreted as resulting from hominid activities (either hunting or scavenging) in combination with natural accumulation of young stegodonts from accidental deaths.

The Liang Bua assemblage differs from mainland assemblages such as Panxian Dadong in representing an island population. This means that a number of transporting taphonomic agents that may act on the formation of a mainland assemblage can be excluded in the case of Liang Bua. For instance, on Flores no non-hominin carnivorous mammal could have hunted or scavenged stegodonts and be responsible for the bone accumulation of a large mammal such as *Stegodon*. There were no porcupines present on the island prior to the Neolithic, though some bones (6.6 per cent) show signs of smaller rodent gnaw marks (Plate 3, fig. 9). Komodo dragons, clearly present in the Pleistocene Liang Bua deposits, may have been involved in the accumulation of *Stegodon* remains inside the cave, besides hominins or natural accumulation by accidental deaths. Komodo dragons did die on the same spot as the stegodonts inside the cave, and predator-generated bone assemblages commonly contain relatively high frequencies of predator bone (Brain, 1981). Komodo dragons are known to prey on juvenile individuals and have been observed waiting until an ungulate like a deer or water buffalo gives birth, after which the newborn animal is swallowed immediately. In case adult prey animals are eaten by komodo dragons, usually only the gut contents remain (Auffenberg, 1981). Passage through the digestive tract of komodo dragons would dissolve all bone tissue, even more so the bones of juvenile stegodonts. In addition, komodo dragons do not carry around carcasses but eat on the killspot, which makes their involvement in the formation of the Liang Bua death assemblage unlikely.

Observations that would speak in favour of hominin involvement in the LB stegodont assemblage are the fact that most stegodont remains are concentrated in two layers with an abundance of stone tools (Morwood et al., 2005: Supplementary Fig. A9) and situated on high ground in sector XI, and the occasional presence of cutmarks, e.g. the vertebra fragment figured in Plate 3, fig. 6. Hominins hunting or scavenging stegodonts would most likely carry parts of carcasses into the cave. The predominance of resistant skull parts (dental elements and petrosals) may be the result of selective loss of the less resistant bones, in particular those of juveniles. Some bones do show dissolution features on one side only (excluding digestion by carnivores), indicating that at least part of the bones may have been lost after deposition, which could explain the under-representation of limb and axial elements and the higher frequency of adult bones in the postcranial assemblage.

## 9. Conclusions

In this paper, a new *Stegodon* subspecies is described from the Late Pleistocene archaeological site Liang Bua on the island of Flores, Indonesia. *S.f. insularis* subspec. nov. is the youngest securely dated *Stegodon* recorded from Southeast Asia and co-occurred with the dwarfed *H. floresiensis*. Both became extinct during a volcanic eruption around 12 ka BP. Considering dental morphology, *S.f. insularis* is the most advanced member of the genus *Stegodon*, with 12 ridges in the lower $M_2$. Compared to its ancestor, *S.f. florensis* known from various sites ranging in age between 850 and 700 ka, *S.f. insularis* is characterized by a linear size reduction of up to 30 per cent and increase in the amount of molar ridges.

In order to explain the death assemblage, one can only conclude that there must have been a very strong selective mortality of young *Stegodon* individuals. The accumulation of *S.f. insularis* remains inside the cave has most likely been the result of hominin activities, either by scavenging or hunting, though alternative explanations of the *Stegodon* bone accumulations cannot be fully ruled out.

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## Appendix A

### A.1. Methods

Measurements are in mm unless otherwise stated. Abbreviations for measurements on molars are: *L*, maximum length of molar at intermediate crown height; *W*, maximum width of molar ("*w*" refers to the width of individual molar ridges); *H*, maximum height of unworn molars ("*h*" refers to the height of individual molar ridges); LF, average of the two lamellar frequencies from both the buccal and lingual side of a molar, measured at the base of the crown. The LF is defined as the number of ridges occurring in antero-posterior direction along 10 cm of the crown base; ET, enamel thickness; *P*, plate formula, which is the number of ridges developed in a complete molar. Incompletely developed anterior and posterior ridges are designated with "x" in front and/or behind the number indicating the amount of fully developed ridges, e.g. "x6x". A "-" in front or behind the ridge number indicates that 1 or more ridges are missing in incompletely preserved molars, e.g "-5x". For measurements on non-dental elements: DAP represents the antero-posterior diameter; DT is the transverse diameter. Measurements followed by "e" are estimated values; molar w and h measurements followed by "(c)" indicate that some buccally or lingually deposited cementum is included in the measurement. Measurement values followed by "+" indicate that the full measurement could not be taken due to incomplete preservation, and that the original value was larger than the given one (Table A1–A3).

## A.2. Description of postcranial elements

### A.2.1. Vertebrae

There are eight identifiable vertebra fragments in the collection, of which four certainly belonged to adult individuals with fused epiphyses. The most complete specimen, ICA-503 h, represents a vertebra lumbale. It consists of a poorly preserved corpus with a portion of the left part of the arcus vertebralis attached but lacking the processus transversalis. The corpus shows considerable superficial damage on the lower left side and posteriorly on the right side, but some measurements could be taken or estimated (Table A4). Another superficially damaged corpus of an adult vertebra lumbale (ICA no. 545) is slightly wider but shorter. The measurements are intermediate between those of adult *S. sondaari* and *S.f. florensis* vertebrae lumbales (Table A4). A posterior vertebra epiphysis of a juvenile individual has a dorsoventral diameter of 56 mm. An isolated processus spinosus (ICA no. 894a) of an adult individual includes a portion of the left side of the arcus, but lacks the tip. It is straight with a preserved length of 150 + mm. It is heavily fractured but has clear irregular tuberosities on both the convex cranial, but more heavily on the concave caudal surface, indicating high age (Plate 3, fig. 7). Another specimen worth mentioning is a right portion of an arcus of a vertebra cervicale with the base of the processus spinosus preserved (ICA no. 11.8.04). Though no standard measurements could be taken on this presumably adult specimen, the outer surface of the arcus shows some parallel cut marks (Plate 3, fig. 6).

### A.2.2. Costa

There are numerous fragmentary and poorly preserved costa fragments amongst the Liang Bua material. Presumably, they mostly are of juvenile *S.f. insularis* individuals. There is a single large portion of an adult costa, which lacks the proximal and distal ends. The curved fragment is 350 + mm long as far as preserved. The fragment has a dorsoventral and antero-posterior diameter at the widest proximal end of 42.5 and 13 mm, respectively. At the distal broken end these measurements are 39.0 and 17.5 mm, respectively. The ventral edge of the rib is sharp, whereas the dorsal edge is rounded. The relatively broad and flattened morphology indicates this rib to be from the anterior region of the thorax.

### A.2.3. Scapula

There are seven scapula fragments represented, of which six belonged to juvenile individuals. A left and a right specimen from spit 43 in sector IV probably belonged to a single individual. One proximal fragment is considerably larger than the others, but the glenoid epiphysis is not yet fully fused. It clearly belonged to an older, subadult individual (ICA no. 26.7.03-2). In most specimens only the minimum transverse and antero-posterior diameter of the collum scapulae could be measured (Table A5). In all six juvenile specimens these measurements are well below those of an adult *S. sondaari* scapula, whereas the subadult specimen ICA-26.7.03-2 is only 10 per cent smaller. In the subadult *S.f. insularis* specimen the minimum transverse diameter of the collum, 28 mm, is similar to that of the scapula of a juvenile *E. maximus* of which the dP3'2 are worn. The latter however, is characterized by a much larger minimum antero-posterior diameter of the collum. Of a juvenile *S.f. insularis* scapula fragment (ICA no. 517a) also the length could be estimated, which amounts to 152e mm. This scapula originates from a concentration of bones and artefacts in sector XI, between a depth of 4.5–4.7 m.

### A.2.4. Humerus

There are only three identifiable humerus fragments in the collection, all belonging to juvenile individuals. A very small left humerus diaphysis (ICA no. 517k) originates from the same bone/artefact concentration as juvenile scapula ICA no. 517a. The proximal and distal ends of the diaphysis are damaged, and it has a length of 131 + mm as far as preserved. The superficial bone of the humerus diaphysis is porous. The lateral epicondylar crest is flattened by parallel rodent gnaw marks (Plate 3, fig. 9). The minimum antero-posterior diameter of the shaft (distally of the crista tuberculi majoris) measures 17.5 mm; the minimum transverse diameter halfway the shaft measures 22.0 mm. The mediolateral diameter of the distal end of the diaphysis measures 58.5 + mm. As the lateral epicondyle shows only superficial damage, the full mediolateral diameter of the distal epiphysis may have been around 60e mm. These measurements correspond with those of a *M. primigenius* foetus in the second year of pregnancy, and are 8–35 per cent smaller than newborn *M. primigenius* calves (Maschenko, 2002). Specimen ICA-517k presumably belonged to an individual in the first year of postnatal growth.

Furthermore, there is a heavily damaged caput humeri of an older but still juvenile individual from the same bone concentration (ICA no. 448d). Its transverse width is

Table A1
*Stegodon florensis insularis* subsp. nov. fossil specimens of dental elements from Liang Bua Cave

| Sector-year/spit | ICA Coll. no. | Element | *P* | *L* | *W* | *H* | L/*W* | ET | *h*/*w* index | LF |
|---|---|---|---|---|---|---|---|---|---|---|
| IV-03/41D | 24.7.03-1 | Right $dP_3$ | 7x | 48e | 26.6 | — | 1.80e | 1.6 | — | 14.1 |
| IV-03/43D | 25.7.03-1 | Molar fragm. | x1- | — | 33+ | 33+ | — | 3.4–3.8 | — | — |
| IV-03/43D | 25.7.03-8 | 5 tusk fragmts. | | | | | | | | |
| IV-03/43D | 25.7.03-2 | Left maxilla+$dP^3$ | x5x/6x | 46.0 | 28.3 | 14.2 | 1.63 | — | 52–61 | 13.8 |
| IV-03/43D | 25.7.03-3 | Left $dP_4$ | x8- | 85.7+ | 36.0 | 28.6 | >2.38 | 2.2–2.3 | 74–85 | 9.5 |
| IV-03/43D | 25.7.03-4 | Right maxilla+$dP^3$ fragm. | -4x | — | 29.4 | — | — | 1.6–1.8 | — | 12.2 |
| IV-03/43D | 25.7.03-5 | Left $dP_4$ fragm. | x3- | — | 29.3+ | 21.2+ | — | — | 72 | — |
| IV-03/43D | 25.7.03-6 | $dI^2$ | — | 6.6+ | 8.0+ | 10.4+ | — | — | — | — |
| IV-01/44s | JR9 | Right $dP_3$ | -6x | — | 25.5e | — | — | — | — | — |
| IV-01/44s | 18.5.01-1 | Left $dP^2$ | 3 | 10.8 | 12.3 | 10 | 0.88 | — | 81.3 | — |
| IV-01/45s | 18.5.01-2 | Right $dP^2$ | 3x | 11.5 | 12.4 | 10.2 | 0.93 | — | 82.3 | — |
| IV-01/45 | 40/JR8 | Left $dP_3$ | x6x | — | 25.5e | — | — | — | — | — |
| IV-01/45s | 45/JR12 | $dP_3$ fragm. | 3- | — | — | — | — | — | — | — |
| IV-03/45D | 26.7.03-1 | $dP^2$ fragm. | 3 | 9.8 | 10e | 8.1 | 0.98e | 1 | 81e | — |
| IV-03/46D | 28.7.03-2 | Right $dP^3$ | 6x/x5x | 42.1 | 26.5e | 15.8 | 1.59e | 1.7 | 55–63 | 14.2 |
| IV-03/46D | 28.7.03-3 | Right $dP^3$ | (x?)6x | 43+ | 30e | — | — | 1.5 | — | 12.4 |
| IV-03/46D | 28.7.03-4 | Left $dP_3$ | -6x | 36+ | 24.5 | — | — | 1.2–1.3 | — | 15.1 |
| IV-01/47 | 5/JR14 | Right $dP_4$ | x8x | 94e | 34e | — | 2.76e | — | — | 9.2e |
| IV-01/47s | 21.5.01-1 | Left $dP^2$ | x2x | 12.2 | 13.8 | 9.2+ | 0.88 | — | — | — |
| IV-01/47s | 4.5.01-2 | Right $dI^2$ | — | 6.6 | 10.0 | 12.8 | 0.66 | — | — | — |
| IV-01/48s | 7.5.01-1 | Right $dI^2$ | — | 6.3 | 8.4 | 9.5 | 0.75 | — | — | — |
| IV-03/48D | 28.7.03-5 | $dP^4$ fragm. | -3x | — | 35.0 | 28e | — | 2.0 | 80e | 9.7 |
| IV-03/48D | 28.7.03-6 | Left $dP^3$ | -5x | 39+ | 32.5 | — | — | 2.0 | — | 12.6 |
| IV-01/49s | 7.5.01-2 | $dI^2$ | — | 7.5 | 9e | 15.0 | 0.83e | — | — | — |
| IV-01/49s | 7.5.01-3 | $dP_2$ | 1 | 7.6 | 10.0 | 8.1 | 0.76 | — | 80e | — |
| IV-03/49D | 28.7.03-7 | Right $dI^2$ | — | 7.0 | 8.8 | 11.6 | 0.8 | — | — | — |
| IV-03/50D | 28.7.03-8 | Right $dP_4$ | -6- | 64+ | 34.2e | 26.4 | — | 2.8 | 75–77 | 10.2 |
| IV-03/51D | 29.7.03-1 | Right $dP^4$ | x7x | 79.2 | 34.8 | 24.7 | 2.28 | 2.9 | 65–76 | 10.2 |
| IV-03/51D | No no. | Milkmolar fragm. | -1- | — | 30e | 22 | — | — | — | — |
| IV-01/51 | 241/7.5.01-4 | $dI^2$ | — | 6.6 | 7.4 | 11.3 | 0.89 | — | — | — |
| IV-01/52s | 30.4.01-1 | $dP_2$ | 2 | 10.1 | 12.3 | 10 | 0.82 | — | 81.3 | — |
| IV-0153s | 8.5.01-1 | Left $dI^2$ | — | 7.5 | 10.0 | 13.2 | 0.75 | — | — | — |
| IV-01/54 | 279b | Right $dP_3$ | x6x | 46.2 | 25.9 | — | 1.78 | — | — | 12.9 |
| IV-01/54s | 8.5.01-3 | Left $dP^3$ | 6x | 42.9 | 28.0 | 13.6 | 1.53 | <1 | 48–55 | 13.5 |
| IV-01/54s | 121/JR15 | Left $dP_3$ | 7x | 48e | 25e | — | 1.92e | — | — | — |
| IV-01/57s | 1.5.01-1 | Right $dP^2$ | 3x | 10.7 | 11.9 | 8 | 0.90 | — | 67.2 | — |
| IV-03/82 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |

Table A1 (*continued*)

| Sector-year/spit | ICA Coll. no. | Element | *P* | *L* | *W* | *H* | L/*W* | ET | *h*/*w* index | LF |
|---|---|---|---|---|---|---|---|---|---|---|
| III-02/38 | No no. | Milk molar fragm. | — | — | — | — | — | — | — | — |
| III-02/39 | 13.7.02-1 | Molar fragm. | x1- | — | 22.1+ | — | — | 0.9–1.3 | — | — |
| III-02/52 | No no. | Enamel fragm. | — | — | — | — | — | — | — | — |
| I-03/17 | 10/5.7.03-1 | Left maxilla + $dP^3$ | x6x | 48.4 | 32.5 | 16.4 | 1.49 | 1.4 | 51–58 | 13.3 |
| I-03/19 | 25/7.7.03-1 | dP4 fragm. | -1- | — | — | 22.4 | — | — | — | — |
| I-03/19s | 7.7.03-2 | dP4 fragm. | -1- | — | 31.6 | — | — | — | — | — |
| I-03/20 | 8.7.03-1 | $dI^2$ | — | — | 8.8 | — | — | — | — | — |
| I-03/20 | 8.7.03-2 | $dP_2$ | x1 | 9.0 | 10.9 | 9.9 | 0.83 | — | 91 | — |
| I-03/20 | 8.7.03-3 | dP3 fragm. | -1- | — | 25.9 | 14.5+ | — | — | 56+ | — |
| I-03/20 | 8.7.03-4 | Molar ridge fragm. | -1- | — | — | 41.1+ | — | 3.6–3.8 | — | — |
| I-03/21 | 8.7.03-5 | Molar ridge fragm. | -1- | — | — | 25.8+ | — | 2.7 | — | — |
| VII-03/42 | No no. | Milkmolar fragm. | -1- | — | — | — | — | — | — | — |
| VII-03/43 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/47 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/48 | No no. | Milkmolar fragm. | — | — | — | — | — | 1.2 | — | — |
| VII-03/48 | LB-JR36 | Molar fragm. | — | — | — | — | — | — | — | — |
| VII-03/54 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/54 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/55 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/56 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/57 | No no. | Milkmolar fragm. | — | — | — | — | — | 0.7 | — | — |
| VII-03/57 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/58 | No no. | Molar fragm. | — | — | — | — | — | 1.5 | — | — |
| VII-03/58 | No no. | Milkmolar fragm. | -2- | — | — | — | — | 0.8–1.0 | — | — |
| VII-03/58 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/58 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/60 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/60 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/60 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/60 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/61 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-03/62 | 3.9.03-1 | dP2 | 2 | 11e | 13e | — | — | — | — | — |
| VII-03/62 | 3.9.03-2 | Molar fragm. | -2- | — | 38+ | 24+ | — | 1.5 | — | — |
| VII-03/63 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-04/63 | VII-63 | Right $M_1$ | x8x | 102 | 35.3 | 27.8 | 2.89 | 1.6–2.6 | 76–79 | 8.8 |
| VII-04/63 | No no. | Molar fragm. | — | — | — | — | — | — | — | — |
| VII-04/63 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-04/64 | No no. | $dI^2$ | — | — | — | — | — | — | — | — |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| VII-03/65 | No no. | Milkmolar fragm. | — | — | — | — | — | — | — | — |
| VII-04/58-72 | 20.7.04R | Left maxilla + $dP^2$ (+ $dP^3$) | — | 9.0 | 12.2 | — | 0.74 | — | — | — |
| VII-04/58-72 | 20.7.04R | left $dP^3$ | 6x | 40.0 | 29.0 | — | 1.38 | 1.4–1.9 | — | 14.3 |
| VII-03/68 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/69 | No no. | Tusk fragm. | — | — | — | — | — | — | — | — |
| VII-03/70 | 8.9.03 | Left $dI^2$ | — | 7.0 | 8.9 | 11.0 | 0.81 | — | — | — |
| XI-04/32 | 2.8.04 | Left $dP^2$ | 3 | 11.6 | 13.7 | 9.7 | 0.85 | — | 71 | — |
| XI-04/35 | XI-35 | Adult tusk fragm. | — | — | 77 | 280 + | — | — | — | — |
| XI-04/37 | 6.8.04 | $dI^2$ | — | 7.7 | 9.0 | 11.1 | 0.86 | — | — | — |
| XI-04/40 | No no. | $dI^2$ | — | — | — | — | — | — | — | — |
| XI-04/40 | No no. | $dP_2$ | — | — | — | — | — | — | — | — |
| XI-04/41 | 9.8.04-1 | dP2 (upper or lower?) | x2x | 12.7 | 11.1 | 10.1 | 1.14 | — | 91 | — |
| XI-04/41 | 9.8.04-2 | Molar ridge fragm. | -1- | | w = 23.0 | — | — | — | — | — |
| XI-04/42 | 309 | $dP_2$ | 2 | 12.0 | 12.2 | — | 0.98 | — | — | — |
| XI-04/42 | 320 | Left $dP_3$ | 7x | 49.2 | 25.2 | 16.7 | 1.95 | — | 60–86 | 14.2 |
| XI-04/42 | 11.8.04 | Left $M^2$ fragm. | x6- | 82 + | 50 | 42e | — | 2.1–2.5 | 84–87 | 7.0 |
| XI-04/44 | 423 | Left $M^3$ fragm. | -9x | 125 + | 59.4 | 50 (+?) | — | 2.9–3.4 | 83–88 | 6.3 |
| XI-04/44 | 421 | Right $dP^3$ | 6x | 47.5 | 30.6 | — | 1.55 | 1.0–1.4 | — | 13.3 |
| XI-04/44 | 402 | Right $dP^4$ fragm. | -4x | — | 34.5 | — | — | 2.2–2.5 | — | 10.0 |
| XI-04/45 | 452b | Tusk fragm. | — | — | 17.3 | 22 + | — | — | — | — |
| XI-04/45 | 456 | Right $M_2$ | x12x | 137 | 45.6c | 42c | 3.00 | 2.6–3.0 | 81–93 | 8.9 |
| XI-04/45 | 452a | Left $dP^3$ | x6x | 49.3 | 30.8 | 17.0 | 1.60 | — | 55–71 | 12.7 |
| XI-04/45 | 454 | dP4? fragm. | 3- | — | $w = 28.3$ | — | — | 1.6 | — | — |
| XI-04/45 | 449b | left $M^1$ fragm. | -4x | 52 + | 40.0 | 28.0 | — | — | 67–71 | 9.3 |
| XI-04/45 | 451a | $M^1$? fragm. | -2- | — | $w = 44.8$ | — | — | 2.5 | — | — |
| XI-04/45 | 447c | Left $dP_3$ | x6- | — | — | — | — | — | — | — |
| XI-04/45 | 16.8.04-1 | Right $dP_2$ | x1x | — | — | — | — | — | — | — |
| XI-04/46 | 505a | Left $dP_3$ | x7x | 46.0 | 25 | — | 1.84 | — | — | 14.8 |
| XI-04/46 | 504a | Right $dP^3$ | 6x | 45e | 28.1 | — | 1.60e | 1.3–1.4 | — | 13.5 |
| XI-04/46 | 507a | Right $dP^4$ | x5- | — | $w = 34.8$ | 24.1 | — | — | 67–73 | — |
| XI-04/46 | 558f | Right $dP_3$ | x7x | 45.4 | 25.1 | 15.4 | 1.81 | 1.2 | 61–77 | 14.7 |
| XI-04/46 | 558e | Right $dP^3$ | 6x | 46.0 | 29.4 | 15 | 1.56 | — | 50–61 | 12.9 |
| XI-04/46 | 503a | Left $dP_3$ | 7x | 51.4 | 27.0 | — | 1.90 | 1.4–1.7 | — | 13.0 |
| XI-04/47 | 521a | Left maxilla fragm. (+ $dp^2$) + $dP^3$ | 6x | 45.0 | 28.2 | — | 1.60 | 1.7–2.0 | — | 13.1 |
| XI-04/47 | 521a | Left $dP^2$ | x2x | 11.2 | 12e | — | 0.93e | 0.9–1.0 | — | — |
| XI-04/48 | 671 | Mandible + right $dP_3$ | x6x | 51e | 28.5 | — | 1.79e | 1.2 | — | 12.5 |
| XI-04/48 | 672 | Mandible + right $dP_4$ fragm. | x5- | 43 + | 28 + | 23 (+?) | — | — | 79–82 | — |
| XI-04/49 | 669a | Left maxilla fragm. (+ $dp^2$) + $dP^3$ | x6x | — | 26.8 | 15.8 | — | 1.2 | 53–63 | 12.6 |
| XI-04/49 | 669a | Left maxilla + $dP^2$ | 3x | 10.8 | 11.1 | — | 0.97 | — | — | — |
| XI-04/49 | 6.9.04-1 | Left $dP^2$ | 2? | — | 10e | — | — | 1.1 | — | — |
| XI-04/49 | 669b | Left $dP_3$ | 7x | 48.5 | 26.5 | 16.3 | 1.83 | — | 59–73 | 13.0 |

Table A1 (*continued*)

| Sector-year/spit | ICA Coll. no. | Element | *P* | *L* | *W* | *H* | L/*W* | ET | *h*/*w* index | LF |
|---|---|---|---|---|---|---|---|---|---|---|
| XI-04/49 | 669c | Left $dP_3$ | 7x | 47.4 | 26.3 | — | 1.80 | 1.5 | — | 14.2 |
| XI-04/49 | 669d | Left $dP^3$ | 6x | 42.8 | 29.5 | — | 1.45 | 1.4 | — | 12.9 |
| XI-04/49 | 669 g | Right $M^1$ fragm. | -8x | 77+ | 41.4 | — | — | 2.0–2.5 | — | 9.7 |
| XI-04/49 | 669 f | Right $M^1$ fragm. | x6- | 57+ | 38+ | 31c | — | 1.7 | 76–84c | 10.6 |
| XI-04/49 | 656 | Right maxilla + $dP^3$ | 6x | 42.5 | 29.3 | — | 1.45 | 1.8 | — | 13.7 |
| XI-04/49 | 655 | Left maxilla + ($dP^2$) + $dP^3$ (same indiv. as 656) | 6x | 43.0 | 30.6 | — | 1.41 | 1.8 | — | 13.7 |
| XI-04/49 | 655 | Left $dP^2$ | x2 | 10.3 | 13.9 | — | 0.74 | — | — | — |
| XI-04/49 | 669 e | Left $dP_3$ | x7x | 49.9 | 27.2 | 16.7 | 1.83 | 1.2 | 61–63 | 12.8 |
| XI-04/50 | 692/693 | Left $dP^3$ | (x?)6x | — | 27.4 | — | — | 1.5 | — | — |
| XI-04/50 | 694 | Right $dP_2$ | x1 | 10.8 | 12.2 | — | 0.89 | — | — | — |
| XI-04/50 | 711 a | $dI^2$ | — | 7.7 | 9.1 | 13.0 | 0.85 | — | — | — |
| XI-04/51 | 757 | 4 small dP fragments | — | — | — | — | — | — | — | — |
| XI-04/52 | 803 a | $dP^3$ fragm. | -4x | 32+ | 28.7 | 15.8 | — | — | 55 | — |
| XI-04/52 | 803 b | dP2 fragm. | — | 12.1 | 12.4 | — | 0.98 | — | — | — |
| XI-04/59B | No no. | Milkmolar fragm. | | | | | | | | |
| XI-04/60B | 865 | Milkmolar fragm. | | | | | | | | |
| XI-04/62B | No no. | Milkmolar fragm. | | | | | | | | |
| XI-04/63B | No no. | Milkmolar fragm. | | | | | | | | |
| XI-04/64B | No no. | Molar fragm. | | | | | | | | |
| XI-04/67 | No no. | Molar fragm. | | | | | | | | |
| XI-04/72 | No no. | Tusk fragm. | | | | | | | | |
| XI-04/73 | 917 | Tusk fragm. | | | 34.5+ | 81+ | | | | |
| XI-04/75A | No no. | Tusk. fragm. | | | | | | | | |
| XI-04/75B | 918 | Tusk fragm. | | | 66+ | 42+ | | | | |
| XI-04/76C | No no. | Tusk fragm. | | | | | | | | |
| XI-04/77A | No no. | Tusk fragm. | | | | | | | | |
| XI-04/77C | No no. | Tusk fragm. | | | | | | | | |
| XI-04/78B | No no. | Tusk fragm. | | | | | | | | |
| XI-04/78C | No no. | Tusk fragm. | | | | | | | | |
| XI-04/79C | No no. | Tusk fragm. | | | | | | | | |
| XI-04/80C | No no. | Tusk fragm. | | | | | | | | |
| XI-04/81C | No no. | Tusk fragm. | | | 32+ | 87+ | | | | |
| XI-04/82 | No no. | Tusk fragm. | | | | | | | | |

The first column shows for each specimen the excavation sector (sectors I, III, IV, VII and XI were excavated), the year of excavation, and the spit level of each specimen. E.g. spit 41 indicates that the specimen was excavated from a depth of between 4.0 a nd 4.1 m. $P$ = number of plates, anterior or posterior half-ridges indicated with x; $L$ = antero-posterior diameter (in incomplete molars the value of the length as far as preserved is followed by "+"); $W$ = maximum transverse diameter (in case of incomplete molars the width value of the largest preserved ridge is followed by "+" ); $H$ = maximum crown height (in case of permanent tusks lacking an enamel crown this value represents the preserved length); ET = enamel thickness, presented as range per molar; $h/w$ index = $100 \times h/w$, the range of unworn individual ridges per molar is given; LF = lamellar frequency, which is the amount of ridges in 10 cm along the longitudinal axis of the molar.

Table A2
S*tegodon florensis insularis* subsp. nov. cranial and mandibular elements from Liang Bua Cave

| Sector-year/spit | ICA Coll. No. | Element |
|---|---|---|
| IV-03/43D | 25.7.03-4* | Right maxilla fragment with $dP^3$ fragment, juvenile |
| IV-01/43D | 25.7.03-7 | Left squamosum fragment with fossa mandibularis and fossa postglenoidalis, juvenile |
| IV-01/43D | 25.7.03-2* | Left maxilla fragment with $dP^3$, juvenile |
| IV-01/47 | 1/21.5.01-1 | Basioccipital fragment, juvenile |
| IV-01/47 | 1/21.5.01-2 | Left os petrosum |
| IV-01/48 | 21.5.01-2 | Right maxilla fragment including inter-alveolar crest, juvenile |
| IV-01/48 | 21.5.01-3 | Right parietal fragment |
| IV-03/49D | No no. | Os petrosum |
| IV-01/53 | 73/23.5.01-3 | Right frontal fragment, incl. processus zygomaticus and crista orbito-temporalis, juvenile |
| IV-01/53 | 73/23.5.01-4 | Left parietal fragment |
| IV-01/54 | 121a/1.5.01 | Left mandible fragment, anterior part of horizontal ramus and symphysis, juvenile |
| IV-01/54 | 279a/1.5.01 | Left mandible fragment, margo alveolaris |
| IV-01/55 | 8.5.01 | Pars orbitalis of right maxilla, juvenile |
| I-03/17 | 10/5.7.03-1* | Left maxilla fragment with $dP^3$, juvenile |
| VII-03/62 | No no. | Os petrosum |
| VII-04/58-72 | 20.7.04R* | Left maxilla fragment with $dP^2$ and $dP^3$, juvenile |
| XI-4/45 | 447d | Left os petrosum |
| XI-04/45 | 448b | Left os petrosum |
| XI-04/46 | No number | Right parietal fragment, subadult or adult |
| XI-04/46 | 517 | Right os petrosum |
| XI-04/47 | 503f | Left mandible fragment; horizontal ramus with alveole for $dP_2$ and $dP_3$, juvenile |
| XI-04/47 | 521a* | Left maxilla fragment with $dp^2$ and $dP^3$, juvenile |
| XI-04/47 | 521b | Left parietal fragment, planum parietale, juvenile |
| XI-04/47 | 521c | Left parietal fragment, planum parietale, juvenile (later ontogenetic stage than previous specimen) |
| XI-04/47 | 521d | Left squamosal with pars temporalis, meatus acusticus spurius, proc. zygomaticus; os petrosum detached, juvenile? |
| XI-04/48 | 623b | Right os petrosum |
| XI-04/48 | 671* | Mandible with right $dP_3$ |
| XI-04/48 | 672* | Mandible with right $dP_4$ fragment |
| XI-04/49 | 655* | Left maxilla fragment with $dP^2$ and $dP^3$ (same indiv. as 656) |
| XI-04/49 | 656* | Right maxilla fragment with $dP^3$ |
| XI-04/49 | 658a | Left os petrosum |
| XI-04/49 | 659 | Right os petrosum |
| XI-04/49 | 669a* | Left maxilla fragment with $dP^2$ and root of $dP^3$ |
| XI-04/50 | 711b | Left os petrosum |
| XI-04/50-65 | 21.9.04-1 | Right os petrosum |
| XI-04/69 | 908 | Right os petrosum |

ICA collection numbers with asterisk are also listed in the previous table.

41+ mm, the antero-posterior diameter amounts to 46+ mm. Also very fragmented is a lateral epicondyle fragment, of a juvenile individual (ICA no. 302). Distally, the undulating surface of the cartilage growth zone is exposed. The antero-posterior diameter of the epicondyle amounts to 65+ mm.

### *A.2.5. Ulna*

A right ulna and radius diaphysis of a juvenile individual (ICA no. 287a) are still articulated (Plate 3, fig. 5). Of the ulna the distal epiphysis was not yet ossified, and proximally the diaphysis is broken at the level of the articular notch with the humerus. Only the lateral coronoid process is preserved. Its articular surface with the humerus is porous and a growth zone was still actively functioning, showing the individual to be a neonate. Length of the diaphysis as far as preserved amounts to 132+ mm. The shaft is strongly curved backwards, a feature also observed in juvenile *M. primigenius* during the first postnatal year (Maschenko, 2002). The minimum transverse diameter of the ulnar shaft measures 22e mm, and its minimum antero-posterior diameter measures 18.7 mm. The distal end of the diaphysis measures 32 mm transversely and 29.5 mm in antero-posterior direction. The posterior surface of the diaphysis is slightly concave transversely at the distal end.

The specimen just described is slightly larger than another juvenile ulna diaphysis fragment (ICA no. 558d; Table A6). Specimen ICA-558d has both coronoid processes broken, but the olecranon is preserved up to the olecranon growth zone, which was not yet fused. The specimen has a preserved length of 122+ mm and a minimum transverse and antero-posterior diameter of 16.0 and 16.8 mm, respectively. The smaller juvenile *S.f. insularis* ulna is of similar size as an ulna of a *M. primigenius* foetus in the last prenatal stage, and smaller than those of neonate calves (Maschenko 2002), and much smaller than adult *S.f. florensis* ulnas (Table A6).

Table A3
Identifiable *S.f. insularis* subspec. nov. postcranial elements from Liang Bua

| Sector-year/ spit | ICA Coll. No. | Element |
|---|---|---|
| IV-03/43D | 25.7.03-7 | Left metacarpus IV, adult |
| IV-03/43D | 25.7.03-9 | Left scapula fragment, juvenile |
| IV-03/43D | 25.7.03-10 | Right scapula fragment, juvenile (same individual as above) |
| IV-03/44D | 26.7.03-2 | Right scapula fragment, (sub)adult |
| IV-01/44 | 16.5.01-1 | *Arcus vertebralis* fragment, juvenile |
| IV-01/45 | 17.5.01-1 | Right tibia diaphysis, juvenile |
| IV-03/45D | 26.7.03-2 | Right uncinatum, adult |
| IV-03/45D | 26.7.03-3 | Left scapula fragment |
| IV-01/48 s | 5.5.01-1 | First phalange fragment, juvenile |
| IV-01/48 s | 5.5.01-2 | Right pelvis fragment |
| IV-01/50 | 2/11.5.01-1 | Right ilium fragment, juvenile |
| IV-01/51 | 3 | Right scapula fragment, juvenile |
| IV-01/52 | 264 | Left femur diaphysis, juvenile |
| IV-01/52 | 75b | Left ulna diaphysis fragment, juvenile |
| IV-01/52 | 252 | Left tibia diaphysis, juvenile |
| IV-01/57 | 287a | Right ulna and radius diaphyses fragments, juvenile |
| IV-01/60 | 89 | Left femur diaphysis, juvenile |
| IV-01/63 | 292 | Right femur diaphysis, juvenile |
| IV-03/73-74D | 21.8.03-1 | Posterior epiphysis fragment vertebra |
| III-02/47 | 17.7.02-1 | Second phalange diaphysis, juvenile |
| VII-03/49 | 27.8.03-1 | Vertebra fragment, juvenile |
| VII-03/63 | 496a | Right metacarpus V, adult |
| VII-03/68 | No no. | Proximal scapula fragment, juvenile |
| VII-03/72 | 545 | Vertebra lumbale fragment, adult |
| XI-04/41 | 302 | Distal humerus fragment, juvenile |
| XI-04/42 | 11.8.04 | Vertebra cervicale arcus fragment, adult?; with cutmarks |
| XI-04/45 | 443e | Carpal? fragment |
| XI-04/45 | 455 | Left scapula fragment, juvenile |
| XI-04/45 | 447b | Left metacarpus V, juvenile |
| XI-04/45 | 448d | Caput humeri, juvenile |
| XI-04/45 | 458 | Caput femori, juvenile |
| XI-04/45 | 446a | Left illium fragment, subadult? |
| XI-04/46 | 18-19.8.04 | Left metatarsus IV, adult |
| XI-04/46 | 517a | Left scapula fragment, juvenile |
| XI-04/46 | 517i | Left metatarsus V, adult |
| XI-04/46 | 517e | Vertebra thoracale, subadult |
| XI-04/46 | 517k | Right humerus diaphysis, juvenile |
| XI-04/46 | 517u | Costa fragment, adult |
| XI-04/46 | 503e | Small vertebra fragment, adult |
| XI-04/46 | 503h | Vertebra lumbare fragment, adult |
| XI-04/46 | 558d | Ulna diaphysis fragment, juvenile |
| XI-04/46 | 558 g | Patella |
| XI-04/47 | 569 | Right metacarpus V, adult |
| XI-04/49 | 660 | Arcus fragment of vertebra |
| XI-04/65 | 894 a | Processus spinosous vertebra thoracale, adult |

Juvenile costa fragments have been omitted from this list.

### A.2.6. Radius

The right juvenile radius in articulation with the ulna mentioned above (ICA no. 287a) has a preserved diaphysis length of 124.5+ mm. The distal end of the diaphysis is attached to the medial surface of the ulna, and has a transverse diameter of 18 mm and an antero-posterior diameter of 28 mm.

### A.2.7. Pelvis

A left ilium fragment (ICA no. 446a; Plate 3, fig. 8) is broken just in front of the iliac spine. It has the tuber sacrale, which was not yet fused, lacking, and the thin crista iliaca and tuber coaxae broken. Thus, the maximum width could not be measured, but amounts to 130+ mm as far as preserved. The small size indicates a juvenile individual. In this specimen, like generally in *Stegodon*, the relatively slender corpus ossis ilium does not expand as rapidly into the ala ossis ilium as it does in *Elephas* or *Mammuthus* (Hooijer, 1955). The minimum mediolateral diameter of the corpus ossis ilium measures 56.5 mm, the dorsal-caudal diameter is 43.5 mm (measurements P4 and P7, respectively, in Van den Bergh, 1999). In the GRDC collection, there is a left pelvis of an adult individual of *S. sondaari*. The specimen (GRDC no. TT4289) was excavated at the locality Tangi Talo in 1999 and has not previously been described. In this specimen, measurements P4 and P7 amount to 59 and 26.5 mm, respectively. In an adult pelvis fragment attributed to *Stegodon sompoensis* from Sulawesi (GRDC no. L-3966/3969; van den Bergh, 1999) measurement P4 amounts to 108e mm. The juvenile Liang Bua specimen thus appears smaller than both adult specimens of other dwarfed stegodonts, though the corpus ossis ilium is relatively thick in antero-posterior direction in the juvenile specimen as compared to adult *S. sondaari*. This difference may be due to a difference in ontogenetic stage.

In another more fragmentary right juvenile pelvis fragment from Liang Bua (ICA no. 5.5.01-2) the ala ossis ilium is broken, but the acetabulum is partly preserved. The posterior margin of the corpus ossis ilium is broken so that measurement P4 cannot be taken, but it measures 42.5+ mm as far as preserved. The estimated value of measurement P4 is ca. 50e mm, slightly smaller than in specimen ICA-446a. The antero-posterior diameter of the fossa acetabulum measures 36 mm.

There is also a posterior margin of a much bigger corpus ossis ilium (ICA no. 2/11.5.01-1), which measures 112+ mm long as far as preserved. Due to the fragmentary status no measurements could be taken, but the fragment belonged to a pelvis of smaller proportions than that of adult *S.f. florensis* specimens.

### A.2.8. Femur

There are three *S.f. insularis* femur diaphyses and one caput femoris in the Liang Bua collection. None of the femur fragments belonged to a full-grown individual, but a left femur diaphysis from sector IV, spit 52 (ICA no. 264; Plate 3, fig. 1), though with unfused epiphyses, is more than 50 per cent larger than the other two diaphysis fragments (Table A7). The femur epiphyses in elephants and woolly mammoths fuse relatively late during ontogeny (Lister, 1999), and possibly the present

Table A4
Measurements (in mm) of adult *S.f. insularis* vertebrae (with fused epiphyses unless otherwise stated) as compared to the two other *Stegodon* species known from Flores

| Taxon | Specimen | Vertebra status | *V*1 | *V*3 | *V*4 | *V*5 | *V*10 |
|---|---|---|---|---|---|---|---|
| *S. sondaari* | GRDC-TT4086 | Thoracale (IV or V) | 40 | 51 | 52 | 51 | 65+ |
| | GRDC-TT4082 | Thoracale (XVI-XVIII?) | — | — | 54 | 38+ | 63e |
| | GRDC-TT4115 | Thoracale | 44 | 47 | — | — | — |
| | GRDC-F.SB-3.2 | Thoracale | 31 | 50 | 56.5 | — | — |
| | GRDC-F.SB-3.3 | Thoracale | 42 | 45 | 52 | 45 | — |
| | GRDC-TT4272 | Thoracale | — | — | — | — | 139+ |
| | GRDC-TT4273 | Thoracale | — | — | — | — | 141+ |
| | GRDC-TT4274 | Thoracale | — | — | — | — | 129+ |
| | GRDC-TT4278 | Thoracale | 39.3 | 56 | 53 | 51 | — |
| | GRDC-TT4283 | Thoracale | 41.5 | 48 | — | 49e | — |
| | GRDC-TT4289 | Lumbale | 44 | 45.5 | 53 | 44 | — |
| *S.f. insularis* | ICA-503 h | Lumbale | 48 | — | 73e | 49e | — |
| | ICA-545 | Lumbale | 43e | 55 | 82e | — | — |
| | ICA-517e | Thoracale | 38.5 | 54 | — | 50 | 82+ |
| | ICA-894a | Thoracale | — | — | — | — | 150+ |
| | ICA-21.8.03 | Thoracale? (juvenile) | — | — | 82+ | 56e | |
| *S.f. florensis* | GRDC-MM3902 | Thoracale | 63 | 83e | 91e | 85e | — |
| | GRDC-MM4121 | Thoracale (XVI-XVIII?) | 61 | 77 | — | — | — |
| | GRDC-MM04-33 | Thoracale | 61 | — | 96.4 | 75 | — |
| | GRDC-MM05-5 | Thoracale (subadult: suture epiphyses visible) | 65.5 | 85 | 102.5 | 82 | 108+ |
| | GRDC-MM05-6 | Thoracale | 59 | 80 | 96.3 | 79 | — |
| | GRDC-MM05-7 | Thoracale | 63 | 81e | 82.7 | 77e | — |

*V*1 = maximum antero-posterior diameter of corpus. *V*3 = dorsoventral diameter of corpus at the cranial articulation fovea; *V*4 = transverse diameter of corpus at the caudal articulation fovea; *V*5 = dorsoventral diameter of corpus at the caudal articulation fovea; *V*10 = length of processus spinosus over the anterior surface, starting at the ventral border of the arcus.

Table A5
Comparison between size measurements (in mm) of *S.f. insularis* scapula fragments and from other Indonesian stegodonts and a juvenile *Elephas maximus*

| Taxon | Locality | Coll No. | Scapula status | *H* | Min. DAP collum | Min. DT collum |
|---|---|---|---|---|---|---|
| *S.f. insularis* | Liang Bua | ICA-3 | Right scapula, juvenile | 133+ | 39 | 18 |
| | | ICA-26.7.03-2 | Right fragment, juvenile | — | 53e | 28 |
| | | ICA-25.7.03-9 | Left fragment, juvenile | 114+ | 39.2 | 15.8 |
| | | ICA-455 | Left fragment, juvenile | — | 36.6 | — |
| | | ICA-517a | Left scapula, juvenile | 152e | 42 | — |
| *Elephas maximus* | ? | NNML | Juvenile (dP3 worn) | 228 | 75 | 28 |
| *S. sondaari* | Tangi Talo | GRDC TT-4291 | Left fragment, adult | — | 45.5+ | 31 |
| *S.f. florensis* | Mata Menge | GRDC MM04-20 | Right proximal fragment | — | 156 | 53 |
| | | GRDC MM04-34 | Left scapula | 535 | 104+ | 58 |
| | | GRDC MM05-30 | Left scapula fragment | — | 150 | 64 |
| *S. trigonocephalus* | Trinil, Java | 13 specimens (Hooijer, 1955) | 15 adult scapulae from Java | 620–720 ($n = 3$) | 150–200 ($n = 15$) | — |

*L* = total height from anterior border of glenoid to upper margin of the spina scapulae; Min. DAP = minimum antero-posterior diameter of collum; Min. DT = minimum transverse diameter of collum. In specimens indicated as adult the glenoid has been fused, in juvenile specimens not. The three specimens from Mata Menge have the glenoid fused.

specimen belonged to a subadult individual. Its length as far as preserved amounts to 310+ mm. The minimum transverse diameter is 48 mm and the minimum antero-posterior diameter is 33 mm (measurements F1 and F3, respectively, of van den Bergh, 1999). The femur lacks the well-developed lateral tuberosities developed on the

Table A6
Size measurements of *S.f. insularis* juvenile ulna fragments as compared to other *Stegodon species*

| Taxon | Locality | Coll No. | Ulna status | *U*3 | *U*4 | *U*9 |
|---|---|---|---|---|---|---|
| *S.f. insularis* | Liang Bua | ICA-558d | Left diaphysis, juvenile | 16.0 | 16.8 | — |
| | | ICA-287a | Right diaphysis, juvenile | 22e | 18.7 | — |
| *S.f. florensis* | Ola Bula | Hooijer (1957): no 125 | Diaphysis, (juvenile?) | <62 | <48 | — |
| | Mata Menge | GRDC-MM4119 | Left diaphysis | 69 | 64 | — |
| | | GRDC MM04-49 | Right ulna | 71 | 65 | 117 |
| | | GRDC MM05-2b | Right ulna | 70 | 71 | 108 |
| | | GRDC MM05-31 | Right ulna | 55.4 | 61 | 94 |
| | Kopo Watu | GRDC-KW3 | Right proximal fragment | 56 | 54 | — |
| *S. trigonocephalus* | Java | Hooijer (1955) | Various specimens from Java | 70–105 ($n = 8$) | — | — |

*U*3 = minimum transverse diameter of diaphysis; *U*4 = minimum antero-posterior diameter of diaphysis; *U*9 = least antero-posterior diameter at neck of joint cavity. Specimens have fused epiphyses unless labelled as juvenile.

Table A7
Comparison between size measurements (in mm) of *S.f. insularis* femurs with other Elephantoid species

| Taxon | Locality | Collection No. | Femur status | *F*1 | *F*2 | *F*3 | *F*7 | *F*8 |
|---|---|---|---|---|---|---|---|---|
| *S.f. insularis* | Liang Bua | ICA-264 | Left diaphysis, juvenile | 48 | — | 33 | 310+ * | — |
| | | ICA-292 | Right diaphysis, juvenile (neonate?) | 21.5 | 17.3 | 13.3 | 150+ * | — |
| | | ICA-89 | Left diaphysis, juvenile (neonate?) | 21.0 | 16.3 | 16.3 | — | — |
| | | ICA-458 | Caput femoris, not fused | — | — | — | — | 75 |
| *Elephas maximus* | | NNML | Juvenile (dP3 worn) | 33.7 | 32 | 26.8 | 325+ * | — |
| *S. sondaari* | Tangi Talo | GRDC TT-4083 | Adult diaphysis | 57 | 38 | 33 | 243+ (460e) | — |
| *S.f. florensis* | Ola Bula | (CV-58; Hooijer, 1972a) | Adult femur | 85 | — | 55 | — | 82.5 |
| | Mata Menge | GRDC MM-4120 | adult (caput fused) | 90 | 55 | 45 | 680+ | 95e |
| | | MM04-42 | Left fragment (prox. part missing) | 90 | 73 | — | 610+ | — |
| | | MM04-46 | Right diaphysis | 95 | 75 | 70 | 395+ | — |
| | Boa Leza | GRDC BL4 | Adult (caput fused) | 81 | 66e | 50e | 666 | 96.5 |
| | Dhozo Dhalu | GRDC DD4188 | Adult (caput fused) | 108 | 75 | 62.5 | 670+ (730e) | — |
| | | GRDC DD4170 | Adult (caput fused, suture still visible) | 105 | 75.5 | — | — | 112 |
| *S. trigonocephalus.* | Trinil (Java) | CD2890 | Adult (caput fused) | 117 | 73.5 | 65 | 922 | 140e |
| | | CD4315* | Adult (caput fused) | 115 | 70 | 63 | 838 | 130e |

*F*1 = minimum transverse diameter of diaphysis; *F*2 = antero-posterior diameter at level of *F*1; *F*3 = minimum antero-posterior diameter of diaphysis; *F*7 = total length of femur. (*: value represents approximately length of the diaphysis excluding both epiphyses); *F*8 = antero-posterior diameter of caput femoris.

distal shaft of the adult femur of *S. sondaari*, *S.f. florensis*, and *S. trigonocephalus*. In an adult femur of *S. sondaari* (GRDC no. TT4083) measurements F1 and F3 amount to 57 and 33 mm, respectively. This suggests that the full-grown femur of the *S.f. insularis* would surpass the size of the adult femur of *S. sondaari*, which is in accordance with the larger size of the milk molars of the Liang Bua *Stegodon*. The isolated caput femoris (ICA no. 458) was not fused yet and is of comparable ontogenetic stage as diaphysis ICA 264. It has an antero-posterior diameter of 75 mm and a transverse diameter of 73.5 mm. In adult *S.f. florensis* femurs, the diameter of the caput measures between 82.5 and 112 mm (Table A7).

Specimen ICA-292 (Plate 3, fig. 2) represents a right femur diaphysis of *S.f. insularis* in a much earlier ontogenetic stage, presumably neonate. Its length is ca. two times smaller than specimen ICA-264. The diaphysis is slender compared to its length, which is normal in very young individuals. Like the even smaller specimen ICA-89, the cross-section of the shaft is tear-shaped, with a sharp longitudinal crest on the lateral surface.

### A.2.9. Tibia

Two *Stegodon* diaphysis fragments are in the Liang Bua collection. A tiny right tibia diaphysis (ICA no. 17.5.01-1) presumably belonged to a neonate individual, whereas the second specimen (ICA no. 252) is considerably larger. The larger left diaphysis has both epiphyses broken. The diaphysis is 214+ mm long as far as preserved. It originates from the same sector and spit as the subadult left femur ICA no. 264, and presumably belonged to the same individual. The tibial crest is already well-developed. The proximal groove for attachment of the fibula is well-developed on the lateral side, but distally the shaft is broken above the sulcus malleolaris. The bone shows a large longitudinal crack over the anterior surface, which is filled with calcareous concretions. Due to this crack, the minimum transverse and antero-posterior diameters can only be estimated (Table A8). The minimum transverse and antero-posterior diameters of diaphysis ICA-252 are between 37 and 48 per cent smaller than in full-grown *S.f. florensis* tibias with fused epiphyses (Table A8).

### A.2.10. Uncinatum

A relatively large uncinatum (ICA no. 26.7.03-2; Plate 3, fig. 3) must have belonged to a full-grown individual. Its dimensions are presented in Table A9 together with those of some other adult proboscidean uncinata, including several specimens from the Soa Basin attributed to *S.f. florensis*. The dimensions of the Liang Bua specimen are 9–29 per cent smaller than those measured in four uncinata of *S.f. florensis*.

### A.2.11. Metapodials

There are four *S.f.* insularis metacarpals and two metatarsals in the Liang Bua collection. Of these six metapodials, five had the distal epiphyses fused. Specimen ICA no. 25.7.03-7 (Plate 4, fig. 4) is a full-grown left metacarpus-IV. The specimen is heavily damaged on the distal side, exposing the spongiose bone, but the epiphysis was clearly fused. It has an estimated total length of ca. 95e mm. Though the length is 17 per cent smaller than in a homologue metacarpal of *E. maximus*, the minimum transverse diameter of the shaft is almost the same. The *S.f. insularis* metacarpus-IV is thus relatively robust, as expressed by the lower Mc1/Mc5 and Mc1/Mc6 ratios (Table A10). This difference was also found between *Stegodon* and *Elephas* metapodials from Sulawesi (van den Bergh, 1999). Also, the metacarpal-IV of *Mammuthus*

Table A8
Comparison between size measurements (in mm) of *S.f. insularis* tibias from Liang Bua and of *S.f. florensis* from the locality Mata Menge

| Taxon | Locality | Spit/collection No. | Tibia status | *T*3 | *T*4 | *T*5 |
|---|---|---|---|---|---|---|
| *S.f. insularis* | Liang Bua, sector IV | Spit 45/ICA no. 17.5.01-1 | right diaphysis, neonate? | 17.8 | 12.4 | — |
| | | Spit 52/ICA no. 252 | left diaphysis, juvenile or subadult (distal epiphysis not fused) | 37e | 32e | 214+ |
| *S.f. florensis* | Mata Menge | GRDC no. MM04-45 | Left tibia fragment | 59 | 56.5 | 340+ |
| | | GRDC no. F/M-3807 | right, adult (both epiphyses fused) | 71 | 62 | 450e |

*T*3 = minimum transverse diameter of diaphysis; *T*4 = minimum antero-posterior diameter of diaphysis; *T*5 = total length.

Table A9
Comparison between size measurements (in mm) of the uncinatum ( = unciforme = os carpale quartum) of *S.f. insularis* from Liang Bua and the uncinatum of other elephantoid taxa

| Taxon | Locality/Coll. No. | Status | *U*5 | *U*6 | *U*7 |
|---|---|---|---|---|---|
| *S.f. insularis* | LB sector IV, spit 45D (ICA no.26.7.03-2) | Right, adult | 55 | 71 | 61 |
| *S.f. florensis* | Ola Bula (Hooijer, 1972) | Right, adult | 60 | 85 | 75 |
| | Boa Leza (Hooijer, 1972) | Right, adult | — | — | 65 |
| | Boa Leza (Hooijer, 1972) | Left, adult | 65e | — | 70e |
| | Mata Menge MM04-25 | Left, adult | 77.4 | 78.5 | 80 |
| *E. maximus* | Zoo NNM-9376 (Hooijer, 1972) | Adult | 74 | 97 | 75 |
| *M. meridionalis* | North Sea; NNM St401526 (Mol et al., 1999) | Left, adult | 132 | 143 | 136 |
| *E.* cf. *antiquus* | Simonelli II Crete (Mol et al., 1996) | Left, adult | — | 104 | 98 |

*U*5 = maximum posterior dorso-ventral diameter; *U*7 = maximum transverse diameter; *U*6 = maximum antero-posterior diameter.

Table A10
Comparison between size measurements (in mm) of a left metacarpus IV of *S.f. insularis* from Liang Bua and of other elephantoid metacarpalia IV

| Taxon | Locality/Coll. No. | Metacarpus IV status | Mc1 | Mc3 | Mc4 | Mc5 | Mc6 | Mc7 | Mc8 | Mc1/Mc5 | Mc1/Mc6 | Mc1/Mc7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S.f. insularis* | Liang Bua; ICA no. 25.7.03-7 | Full-grown (epiphyses fused) | 85.5+ (95e) | 48e | 47e | 39 | 32 | 52e | 35+ | 2.44e | 2.97e | 1.83e |
| *S.f. florensis* | GRDC no. MM05-10 | Full-grown (epiphyses fused) | 113.6 | 66.0 | 64e | 55.3 | 39.4 | 66.4 | 57.5 | 2.05 | 2.88 | 1.71 |
| *S. zdanski* | Zheng et al. (1975) | Adult (both epiphyses fused) | 202 | 123 | 127 | — | — | 140 | 110 | — | — | 1.44 |
| *E. maximus* | Zoo skeleton in NHMN | subadult (dP4/*M*1 worn; distal epiphysis not yet fused) | 115 | 53 | 59 | 42.6 | 31.5 | — | — | 2.70 | 3.65 | — |
| | Zoo skeleton in NHMN | juvenile (dP3 worn, both epiphyses not yet fused) | 60 | — | — | 23.2 | 19.1 | — | — | 2.59 | 3.14 | — |
| *M. meridionalis* | NHMN St.118653 | adult (Mol et al., 1999) | 223 | 95 | 119 | 80 | 66 | 109 | 104 | 2.79 | 3.38 | 2.05 |
| | Coll. Mol, no. 1066 | Juvenile/subadult (distal epiphysis not yet fused) | 147+ | 92 | 107 | 84 | 63 | 94e | 93 | — | — | — |

Mc1 = total length; Mc3 = DT proximal; Mc4 = DAP proximal; Mc5 = minimum DT diaphysis; Mc6 = minimum DAP diaphysis; Mc7 = maximum DT distal; Mc8 = maximum DAP distal.

Table A11
Comparison between size measurements (in mm) of *S.f. insularis* metacarpalia-V from Liang Bua and of other elephantoid metacarpalia-V

| Taxon | Locality/Coll. No. | Metacarpus V, status | Mc1 | Mc2 | Mc3 | Mc4 | Mc5 | Mc6 | Mc7 | Mc8 | Mc2/Mc5 | Mc2/Mc7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S.f. insularis* | LB; sector VII, spit 63; ICA no. 496a | Dextral, full-grown | 81e | 64 | 43+ | — | 33 | 33 | — | 40e | 1.94 | — |
| | LB: sector XI, spit 45; ICA no. 447b | Sinistral, distal epiphysis not fused | — | — | 48 | 44 | 33 | 37 | — | — | — | — |
| | LB; sector XI, spit 47; ICA no. 569 | Dextral, full-grown | 71 | 53 | 32+ | 33e | 30.5 | 31 | 36.5 | 35 | 1.74 | 1.45 |
| *S. zdanski* | Zheng et al. (1975) | Full-grown | 202 | — | 130 | 121 | — | — | 121 | 113 | — | — |
| *Elephas spec.* | South Sulawesi, GRDC TA3062 | Dextral, full-grown | 145 | 128 | 85 | 78 | 58.5 | 54 | 81 | 73 | 2.18 | 1.58 |
| *M. meridionalis* | Coll. Mol no. 2020 | Sinistral, full-grown | 189 | 150 | 96e | 114 | 91 | 109 | 101 | 111 | 1.65 | 1.49 |
| | NHMN no. St119044 | Sinistral, full-grown | 201 | 156 | 94 | 113 | 84 | 104 | 97 | 115 | 1.86 | 1.61 |
| | NHMN no. St118676 | Dextral, full-grown | 182 | 153 | 88 | 102 | 65 | 81 | 84 | 95 | 2.35 | 1.82 |

Definitions of measurements and data for *M. meridionalis* taken from Mol et al. (1999). Mc2 = length between proximal and distal articulation surfaces; other measurements: see Table A10.

Table A12
Comparison between size measurements (in mm) of a *S.f. insularis* metatarsus IV from Liang Bua and of *S.f. florensis* from Mata Menge

| Taxon | Locality/Coll. No. | Metatarsus IV, status | Mt1 | Mt3 | Mt4 | Mt5 | Mt6 | Mt7 | Mt8 |
|---|---|---|---|---|---|---|---|---|---|
| *S.f. insularis* | ICA no. 18-19.8.04 | Sinistral, full-grown | 73e | 46.7 | 41.7 | 34.0 | 29.3 | 46.4 | 41.4 |
| *S.f. florensis* | Mata Menge; GRDC MM04-22 | Dextral, full-grown | 76.0 | 43.5 | 45.0 | 37.8 | 31.1 | 46.7 | 39e |

Measurement numbers (with prefix Mt) are the same as for metacarpals, see Table A10.

*meridionalis* is more slenderly built as compared to *S.f. insularis*. Compared to its larger ancestor, *S.f. florensis*, the metacarpal-IV of *S.f. insularis* is slightly more slenderly built.

There are three *S.f. insularis* metacarpalia-V from Liang Bua: ICA nos 496a (Plate 4, fig. 2), 447b (Plate 4, fig. 3) and 569 (Plate 4, fig. 5). In specimen ICA-447b the distal epiphysis is lacking. In specimen ICA-496a, the anterior edge of the proximal articulation surface is damaged as well as the posterior surface of the distal hinge joint. Most complete is specimen ICA-569, with only some damage on the medial surface of the shaft.

The difference between the robust *Stegodon* and more slenderly built *Elephas* or *Mammuthus* is less clear in the metacarpus-V, and overlap exists between the ratios between the length and minimum transverse or antero-posterior diameter (Table A11). Theoretically, it is expected that the proportions of the metacarpal-V are subject to more variability on the genus and even species level, because the degree of reduction of the lateral finger is in different stages amongst the various taxa.

A left metatarsus-IV (ICA no. 18-19.8.04) is full grown with the distal epiphysis fused. The specimen is of comparable size as a homologue metatarsus of *S.f. florensis* from the locality Mata Menge (Table A12).

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