Elephantoidea in the Indonesian region: new *Stegodon* findings from Flores

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SUMMARY: Recent discoveries of fossil *Stegodon* remains from the island Flores (Nusatenggara, Indonesia) are discussed. The findings confirm earlier discoveries from that island. An Early Pleistocene fossil island assemblage, dated at 0.9 Ma, contains the dwarfed *Stegodon sondaari* in association with *Varanus komodoensis* and giant tortoise remains. A Middle Pleistocene assemblage discovered at numerous localities and dated between 0.85 and 0.7 Ma, contains the intermediate to large-sized *Stegodon florensis*, the giant *Hooijeromys nusatenggara* and *V. komodoensis*. This fauna is associated with early humans as evidenced by the occurrence of stone tools at various localities. A juvenile skull of *S. florensis* shows that this species is closely related to the *S. trigonocephalus* group.

1. INTRODUCTION

Fossil Elephantoidea are important elements in each of the successive faunal units on Java. Their fossil remains are common in the vertebrate-bearing strata and they are good biostratigraphic indicators. Because of their great potential to colonize islands, fossil elephantoids are also frequently encountered on other islands in the region, which enhances their importance for biostratigraphic correlations of terrestrial deposits amongst the various islands.

Following the emergence of Java above sea-level from the Late Pliocene until ca. 1.5 Ma, mammalian dispersal to Java was limited. This is illustrated by impoverished faunal assemblages and the occurrence of various dwarfed elephantoids in this time interval, indicating isolated conditions. The earliest known well documented fauna from Java, the Satir fauna (2-1.5 Ma) contains a mastodon of Chinese origin, *Sinomastodon bumiajuensis*. There are no predatory mammals known from this fauna. Further uplift and volcanic activity in combination with episodes of low sea-level led to an increasing accessibility of the Java region between 1.5 and 0.8 Ma. *Stegodon* (*S. elephantoides* and *S. trigonocephalus*) appears to be the only Elephantoid genus present on Java around that time. The associated faunas (Ci Saat and Trinil Faunas, the latter including *Homo erectus*) are somewhat impoverished, suggesting filter dispersal. Corridor dispersal to Java occurred for the first time between 0.8-0.7 Ma. This time interval concurs with the arrival of the first modern, high-crowned *Elephas* (*E. hysudrindicus*) on Java. Only during the Late Pleistocene does *Elephas maximus* enter Java, associated with the first recorded rainforest fauna. *Stegodon* becomes extinct around that time. *E. maximus* becomes extinct on Java during the Holocene.

Evidence from Sulawesi and Flores indicates that those islands remained isolated from the mainland and from Java throughout the Quaternary. On both islands we find a succession of distinct endemic island faunas with dwarfed Elephantoids until the Middle Plei-

stocene. Around the early Middle Pleistocene these dwarfed Elephantoids are replaced by new immigrants of large- to intermediate size. Presumably, a period of prolonged low sea-level around 0.8 Ma led to an increased accessibility of these islands, though the associated faunas demonstrate a continued isolation. *Stegodon* remains are also known from the islands Timor, Sumba and various Philippine islands, but stratigraphic control is less accurate on these islands.

2. STEGODON FAUNAS FROM FLORES

On Flores a late Early Pleistocene island fauna with the very small *Stegodon sondaari* is replaced by a Middle Pleistocene island fauna with the medium to large-sized *Stegodon florensis*. *Stegodon sondaari* is the smallest elephantoid from the Indonesian region so far discovered, with an estimated bodyweight of around 300 kg (van den Bergh 1999). It occurs in a fossiliferous layer at the locality Tangi Talo, which has been dated by means of paleo-magnetism and fission-track dating at 900 + 70 ka (Sondaar *et al.* 1994; Morwood *et al.* 1998, 1999). *S. sondaari* co-occurs with the still extant Komodo dragon, *Varanus komodoensis*, and a giant tortoise. The enamel microstructure of *S. sondaari* shows some primitive characteristics. On the other hand it possesses some derived characters in the form of increased hypsodonty and relatively large molar wear surface. This adaptation has evolved independently in various island stegodonts, whereas mainland stegodonts have remained very conservative in their brachyodont molars. Increased hypsodonty may be an adaptation to increased wear of the molars, because foraging should have been closer to the ground and the food more contaminated with sand and grid. Alternatively, the dwarfed island stegodonts may have been forced to include more tough grasses into their diet under the strong seasonal conditions on Flores.

In younger layers *S. sondaari* and tortoises have disappeared. These younger layers contain the intermediate to large-sized *Stegodon florensis*, known from a wide range of localities spanning a time interval of between 850 and 700 ka. Humans, as evidenced by artifacts, co-occur with *S. florensis* in some of the localities ranging in time between 840 – 700 ka (e.g. Boa Lesa, Mata Menge, Kobatuwa; Morwood *et al.* 1998, 1999). This suggests that *Homo erectus* was already able to cross limited sea-barriers at a very early stage.

3. NEW FINDINGS FROM FLORES

Recently, new fossil material of both *Stegodon* species has been collected from the Soa Basin, Ngada District, West Central Flores, during 4 successive fieldworks between 1996 and 1999. The material was recovered during a geological/archaeological study in the area carried out by a joint team composed of members from the Geological Research and Development Centre (GRDC) at Bandung, Indonesia, the University of New England, Armidale, Australia, and the National Institute of Archaeology (ARKENAS) at Jakarta, Indonesia.

Amongst the newly discovered *S. sondaari* material from Tangi Talo are some complete molar elements and fragments of postcranials not previously recorded. Postcranial elements of *S. sondaari* are pelvis and scapula. Also some relatively large tusk remains have been collected. The tusks appear to have been extensively used as shown by heavy abrasion on the ventro-medial surfaces, presumably for digging (waterholes, edible roots?). The material also contains a mandible with both the left and right dentition preserved (TT4255). At both sides a small completely worn remnant of the dP_4's in front is still unshed, followed by the half worn M_1's. Of the left side the ascending ramus is preserved with an anterior fragment of the M_2 under formation still in the alveole. The dental wear pattern allows to attribute the mandible to dental wear stage dP4/M1-C, age class 1 (van den Bergh 1999). The individual was slightly younger than that of the holotype mandible, in accordance with its slightly smaller size (Fig. 1).
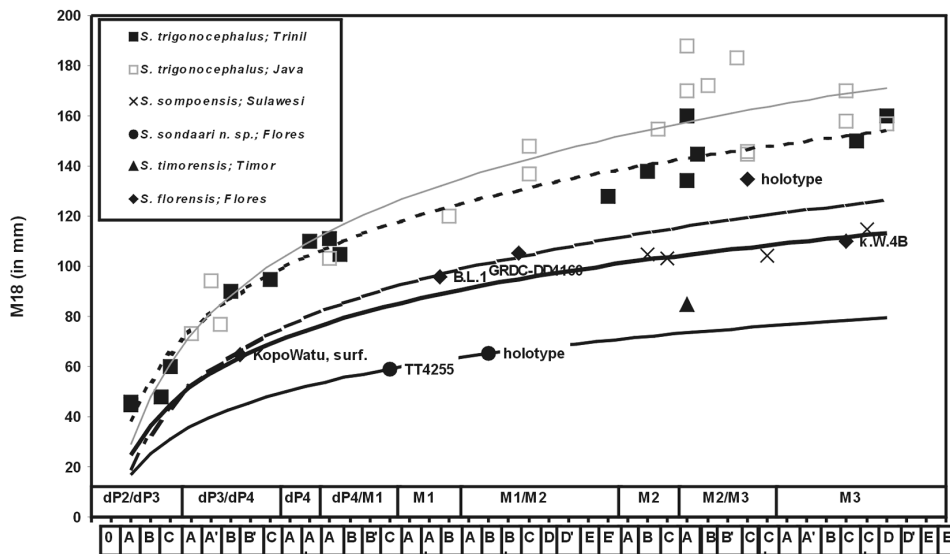
Fig.1 - Maximum transverse diameter of the mandibular horizontal ramus as a function of dental wear age class for various *Stegodon* species from Indonesia (for more details on the methods see van den Bergh *et al*. 1999).

The prize specimen from the 1996-1999 collection is certainly an almost complete juvenile skull of *S. florensis* from the locality Kopo Watu. There are also several mandibles with dentition amongst the newly collected material. The skull, with the catalogue number K.W.1, is the first skull of *S. florensis* on the record. The dentition is preserved on both sides and consists of both worn dP⁴'s and the unworn M¹'s. The state of wear allows to ascribe the present individual to Dental Wear Age Class dP⁴-A', or age group 1(juvenile; see van den Bergh 1999). The individual was slightly younger than the type skull of *S. trigonocephalus*, in which the first ridges of the M1's are worn. The similar age class allows a good comparison between the two species. It follows that the size of specimen K.W.1 is a little smaller than the slightly older individual of the *S. trigonocephalus* type skull. The skull is smaller than the adult skull of the dwarfed *S. sompoensis* from the Walanae Fauna in South Sulawesi. The morphology of the present skull shows great resemblance with that of *S. trigonocephalus*. The wide fronto-parietal region with a wide nasal opening, and the pear-shaped depression between the cresta orbitotemporalis and the cresta orbitalis ven-

tralis indicate a close relationship between the two species. Major differences are the more advanced molars. The molars are more hypsodont (though this could not be verified in the present skull), and homologue molars may have one ridge more than in the subspecies *S. trigonocephalus trigonocephalus* from the Javanese localities Trinil and Kedung Brubus (Tab. 1). Note that in *S. trigonocephalus ngandongensis* from the Late Pleistocene Javanese localities Ngandong, Watualang and Grenjengan (van den Bergh 1999) the ridge crest formula is even more advanced than in the Middle Pleistocene *S. florensis*. Furthermore, skull K.W.1 exhibits a retracted nuchal crest with a weak tendency of the parietals to become inflated. The latter feature is even more developed in *S. orientalis*, in which the adults have a pair of prominent domes on the vertex of the skull (Saegusa 1993). However, *S. orientalis* differs from the present skull in having a total loss of the nuchal crest and the development of a shallow groove on the forehead. The slightly inflated parietals in specimen K.W.1 more likely represents a juvenile character. *S. florensis* appears closely related to the *S. trigonocephalus* group.

Tab.1 - Ridge crest formulas of various *Stegodon* (sub)species from Indonesia.

		dP2	dP3	dP4	M1	M2	M3
S. sondaari	Upper	-	6-7	6	6-7	-	8
	Lower	-	6	-	8	8	8
S. florensis	Upper	-	-	6	7	-	12
	Lower	-	-	7-7+	8-9	10	14
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+	-	-

Inclusion of the newly collected dental material in the death assemblage of *S. sondaari* from Tangi Talo (Fig. 2) confirms the earlier hypothesis that this assemblage reflects the structure of a living population (Haynes 1991; van den Bergh 1999). It seems that non-selective mortality affected an entire population, including prime-adults. In combination with the nature of the layer in which the fossils are found (a tuffaceous layer with abundant pumice), a catastrophic volcanic eruption is the most likely cause for the death of the animals. The time-averaged composite death assemblage of *S. florensis* is dominated by senior and very old individuals, together comprising 42% of the minimum number of individuals, which is more than the total percentage of the juvenile age group (35%). The assemblage may be biased because the material includes specimens described by Hooijer (1967, 1972), who may have preferentially described the easily recognizable tapering M3's. An explanation for the relative high percentages of old individuals could be that living conditions on Flores were quite optimal and that mortality amongst the juveniles and prime-aged individuals was exceptionally low. But other explanations, such as selective removal of juveniles from the assemblage by predating komodo dragons can also be put forward. How the proven presence of humans fits in is not clear at the moment. So far no evidence for butchering sites has been found in the Soa Basin.
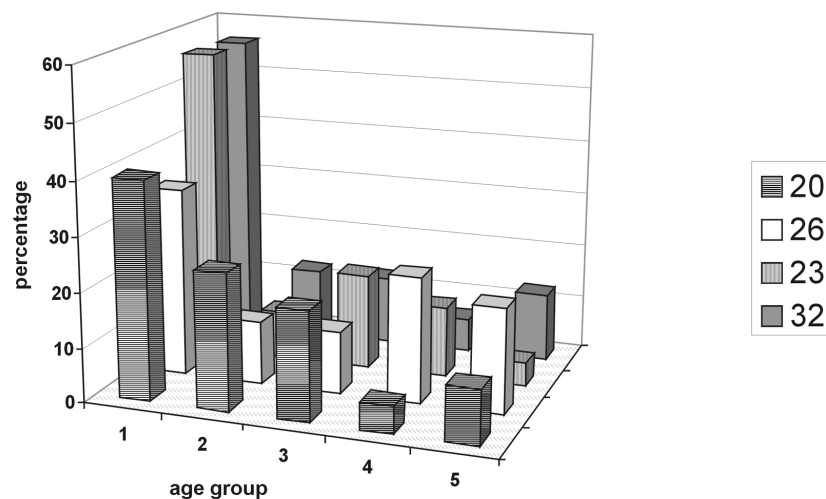

Fig.2 - Age profiles of fossil Elephantoid assemblages from various localities in Indonesia. Legend indicates the minimum number of individuals on which each profile is based. From front to back: *S.sondaari* from the locality Tangi Talo; *S. florensis* from various localities in the Soa Basin, Flores; *"Elephas" celebensis* from

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4. ACKNOWLEDGEMENTS

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6. POSTSCRIPTUM

During a recent excavation in the cave Liang Bua, for the first time *Stegodon* fossils have been discovered in a cave setting on Flores. Previous excavations in Liang Bua had yielded Neolithic and Metal age graves in the uppermost 2.2 m of the cave floor, underlain by Mesolithic and then Palaeolithic stone artefacts to a minimum depth of 4.25 m. The recent excavation reached a maximum depth of 6.8 m and yielded the remains of an archaic hominid population, stone artefacts, *Stegodon*, giant tortoise, pig, deer and Komodo dragon in the basal levels. This deposit is overlain by 3 lenses of tuffaceous silt, providing a potential source for dating (Morwood *et al* 2001). The remains of at least 3 juvenile *Stegodon* individuals seem to be involved, but a detailed study of the material has still to be done.