Pleistocene Reptiles of The Soa Basin (Flores, Indonesia): Adaptation and Implication for Environment

Reptil Plistosen Cekungan Soa (Flores, Indonesia): Adaptasi dan Implikasi Terhadap Lingkungan

Erick Setiyabudi

Geology Museum, Bandung
Jalan Diponegoro 57, Bandung, Indonesia
Email: erick_91119@yahoo.com

Abstract - The presence of fossil reptiles from the mainland of Asia, such as: giant tortoise (*Megalochelys* sp.), fresh water turtle (Geoemydidae), crocodile (*Crocodylus* sp.) and the komodo dragon (*Varanus komodoensis*) in the Soa Basin of Flores, supports the hypothesis that Wallace's line is not a demarcation line between the reptilian fauna from Asia (Indo-Malayan region) and that from Australia (Austro-Malayan region) in the reptiles came to Flores about 1 million years ago, or perhaps earlier (during the Pleistocene), by sweep stake dispersal through swimming or floating. After arrived, they lived in isolated conditions and adapted to a savannah environment. Nevertheless no morphological changes with their Asian mainland ancestors could be found.

Keyword - *Megalochelys* sp., *Crocodylus* sp., *Varanus komodoensis*, sweep stake, Isolation, Savannah.

Abstrak - *Kehadiran fosil reptil dari daratan Asia, seperti: kura-kura raksasa (Megalochelys* sp.*), kura-kura air tawar (Geoemydidae), buaya (Crocodylus* sp.*) dan komodo (Varanus komodoensis), dari Cekungan Soa Flores, mendukung hipotesis bahwa garis Wallace bukan garis demarkasi antara fauna reptil dari Asia (kawasan Indo-Malaya) dan berasal dari Australia (kawasan Austro-Malayan) pada reptil sampai ke Flores sekitar 1 juta tahun yang lalu atau mungkin sebelumnya (selama Plistosen), dengan penyebaran bersifat untung-untungan dengan cara berenang atau mengapung. Setelah tiba, mereka hidup dalam kondisi terisolasi dan menyesuaikan dengan lingkungan savanna. Namun demikian tidak terdapat perubahan morfologi dengan nenek moyang mereka dapat ditemukan di daratan Asia.*

Kata Kunci - *Megalochelys* sp*., Crocodylus* sp*., Varanus komodoensis, bersifat untung-untungan, Isolasi, Savanna.*
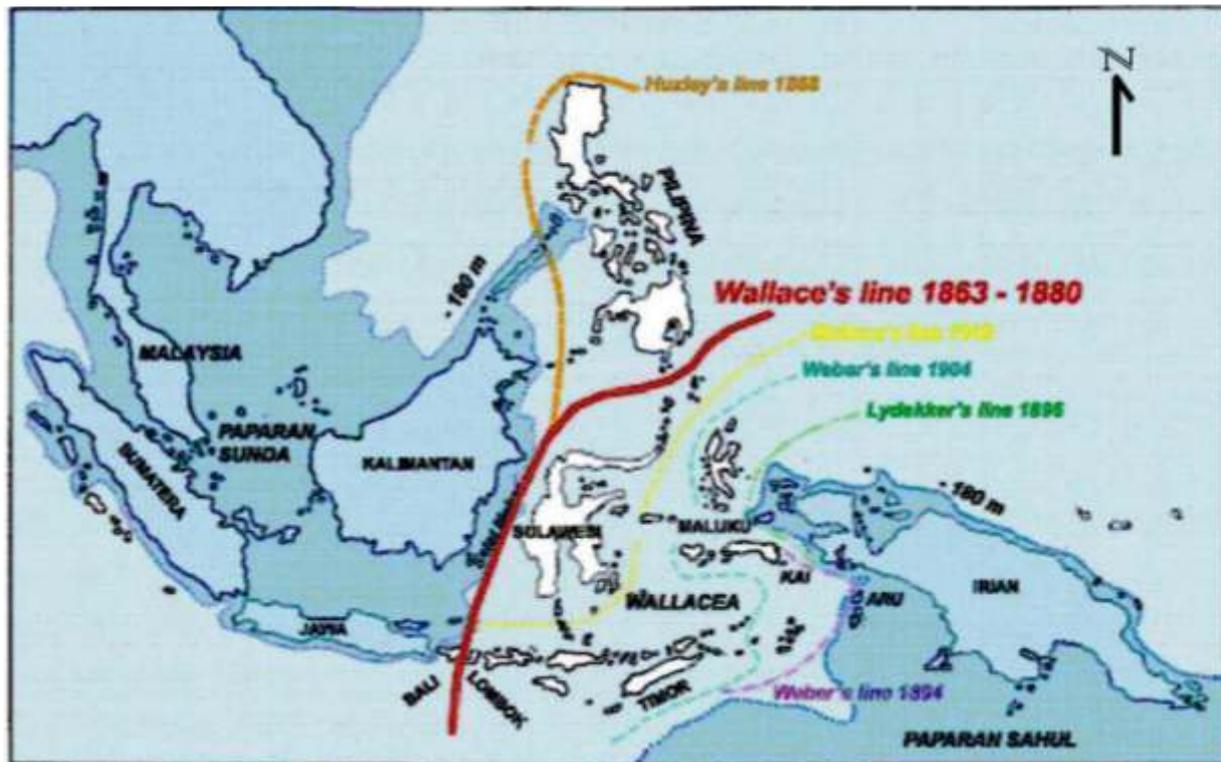
Sources : modified by Aziz, 1990 after George, W., 1981

**Figure 1.** Wallace's line and Flores Island

INTRODUCTION

Flores is one of the islands of the Wallacean Archipelago, which is located opposite to the east line of Wallace, dividing the fauna with an Asian origin of the Indo-Malayan region and the fauna from Australia, the Austro-Malayan region (Wallace, 1863) (Figure 1). The first vertebrate fossils fauna from the Soa Basin, Flores was discovered by king Nagekeo , Joseph Djuwa Dobe in the Ola Bula area in December 1956, were reported by Hooijer (1957) as *Stegodon trigonocephalus florensis*, which was supposed to be a subspecies of *Stegodon trigonocephalus* of Java. Nowadays the Flores species is called *Stegodon florensis* (Maringer & Verhoeven, 1970). However, the proboscidean *Stegodon* has the ability to swim very well. Though, it is not a surprise that *Stegodon* fossils are found on the islands of Wallacea, like Sangihe, Sulawesi, Sumba, Flores and Timor (Hooijer, 1949, 1957; Sartono, 1969; Sondaar, 1987; Aziz, 1990, 1994, 2000). The first fossil reptile in the Soa Basin was recognized from Tangi Talo site (previous called Bhisu Sau), around 31m below the horizon of *Stegodon florensis* in the old village (*Kampung Lama*) Ola Bula, was found by Sondaar in the form of a giant tortoise, which was identified as *Geochelone* sp. (Sondaar, 1987).

Moreover, the reptil fossil of Wallacea were also reported from outside island of Flores such as Walanae South Sulawesi (Hooijer, 1948; Aziz, 1990, 1994), Timor (Hooijer, 1971,1972), and Sumba Islands (Setiyabudi, *et al.*, 2012). In Flores, Brongersma (1958) described fossil materials from cave Holocene deposits as *Varanus hooijeri*, other several materials of Soa Basin were identified as *Varanus komodoensis* (Hocknull *et al.* 2009).

Systematic excavation in the Soa Basin Flores were carried out (1991-2015) during join research between the Geological Agency and the University of Utrecht, Biodiversity Centre Leiden, the Netherland, the University of New England and the University of Wollongong, Australia resulted in thousands of various vertebrate fossils and stone tools.

Vertebrate fossils are dominated by the extinct proboscidean (*Stegodon* sp.), which reached more than 85% and reptile about 10% in fossil populations. The reptile fossils consist of giant tortoise, komodo, fresh water turtle and crocodile.

Owing in the presence of reptile fossil materials from Soa Basin, some attempts have been made to understand. Thus this paper presents limited reptiles fossil of the Soa Basin and discusses their adaptation aspects concomitant with environments.
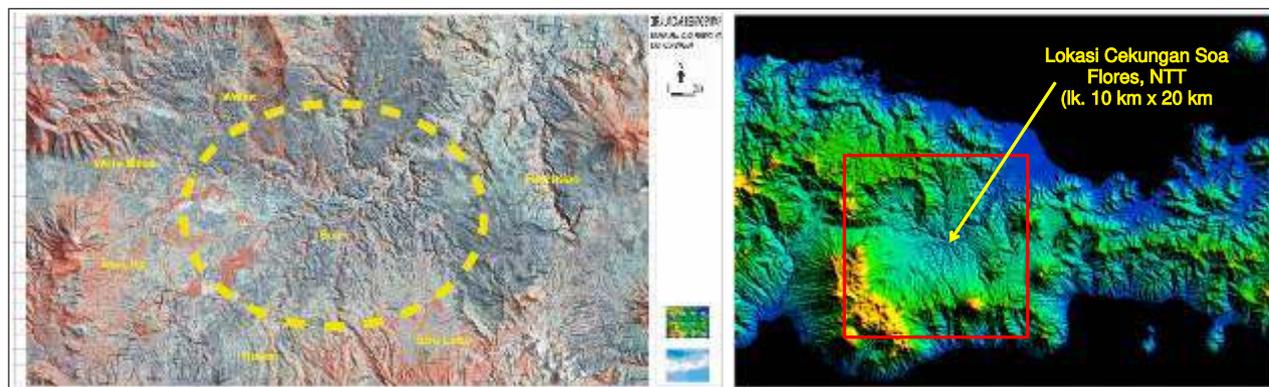
Figure 2. Satellite Image of the Soa Basin.

MATERIAL AND METHOD

Materials were used latest study come from the joint research (1991 – 2015) of the systematic excavation, almost 50 trenches (2010-2015) in several sites of Soa Basin. We found fossil materials in the four paleontological sites of 16 potential fossil sites in the Soa Basin, such as Mata Menge (MM), Dozo Dhalu (DD), Tangi Talo (TT), and Kobatua (KT). More than thousands fragment vertebrate fossil specimens were collected and housed in the Geological Museum Bandung (MGB), Indonesia. The most of fossils are fragmented, however some of them a good preservation.

Previous numbers of some materials especially giant tortoise *Megalochelys* sp. specimens were collected from the tuff deposits of the Tangi Talo (TT) excavation during 1991-1993 that reported by Sondaar *et al.* (1994), van den Bergh et al. (2001), Aziz, *et al.* (2009).

We documented fossil reptile specimens of Soa Basin, which are labeled as field registration in the format of locality with trench number, year, and find number. The field registration has been adopted into database processed in MGB. However, exact total numbers of fragmental fossil materials of each taxon has not been calculated yet for statistic purposed, it has been under preparation and reconstruction.

Morphological comparisons with the present fossils were conducted relevant data for the other living and fossil testudinid, geoemydid, komodo, and *Crocodylus porosus*. Morphological data were also taken from previous literatures. The fossil reptile materials were measured by using digital Mitutoyo vernier calipers to the nearest 0.1 mm. All measurements were taken at the widest or longest portion of each dimension. The turtle terminology follows Zangerl (1969), komodo (Conrad, 2008), and crocodilian (Grigg and Gans, 1993).

GEOLOGY AND STRATIGRAPHY OF THE SOA BASIN

The Soa Basin is located in central Flores, the coordinates are S 08° 39' 00"- S 08° 46' 00", and E 120° 03' 00"- E 121° 13' 00" belonging to the administrative area of the Ngada and Nage Keo Regencies. The geological map of Soa Basin were first executed by Ehrat (1925) and it was said that the Soa was a plateau. Hartono (1961) investigated geology and stratigraphy of Soa Basin in response to discoveries of *Stegodon trigonocephalus florensis* (Hooijer, 1957). Furthermore, geological research and detailed stratigraphy was observed by Suminto *et al.* (2002). Analysis and interpretation of satellite as well as field observations show that the Soa region is an ancient volcanic caldera (Soa Caldera) and will be further in this paper called the Soa Basin. This basin dimension is an approximate 20km x 20km. Its area is surrounded by a number of volcanoes, both active and inactive, among others: Ebu Lobo, Keli Lambo, Keli Eli and Eni Rie with the Ae Sissa main river with tributaries: Lowo Labo, Lowo Hwa, Lowo Lele, Wae bha and Wae Nangge (Aziz, *et al.,* 2009) (Figure 2).

The Soa Basin was filled by three formations (Figures 3 & 4), in ascending order from old to young: the Ola Kile and Ola Bula Formations, and the young volcanic rocks. A huge explosive volcanic eruption occurred at about 2.5 Ma, sourced from the Welas volcano in the northern part of the basin (Muraoka *et al.,* 2000). This product of eruption was considered as source rock of the basement bedrock and comprises massive and resistant andesitic breccias and volcanic mudflows with lava flows that we call Ola Kile Formation (Aziz, *et al.,* 2009). A fission-track date from near the top of the Ola Kile Formation has a minimum age of 1.86 ± 0.12 Ma (O'Sullivan, *et al.*, 2001).
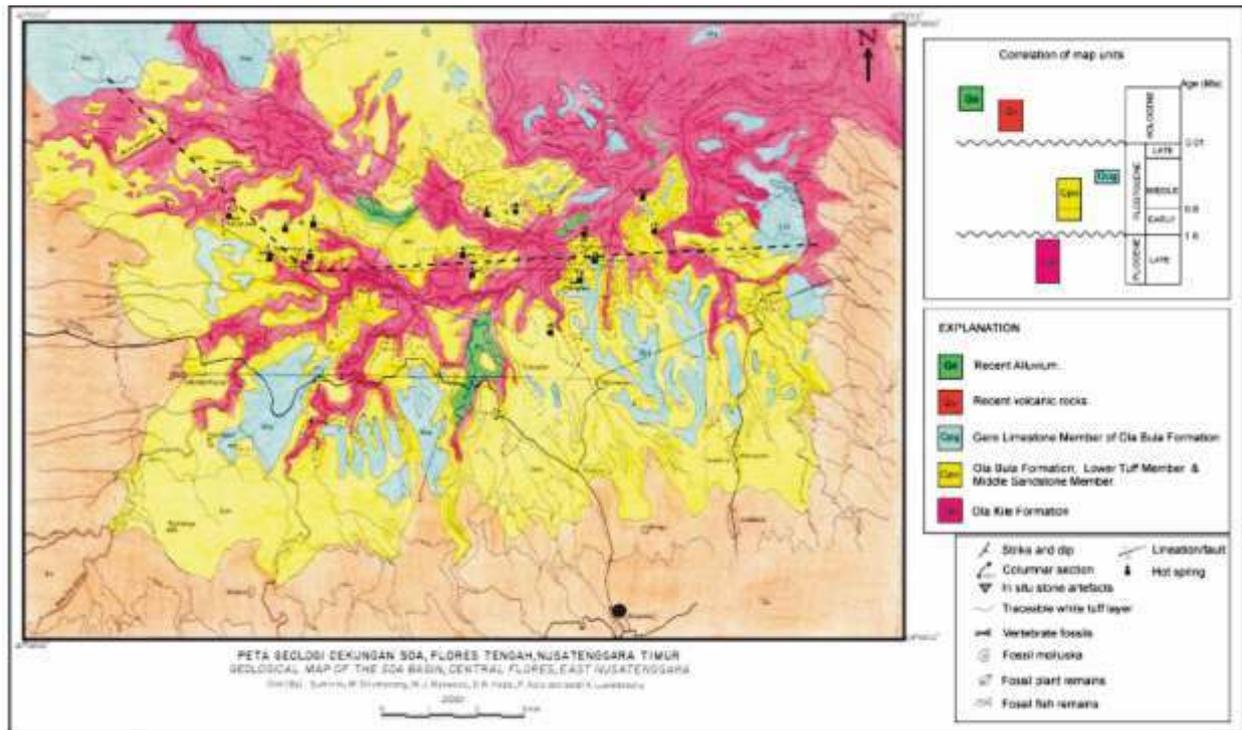
Sources : Aziz, et al., 2009

Figure 3. Geological Map and Paleontological sites of the vertebrate fossil in the Soa Basin 1 . *Kobatuwa*; 2 .*Mata Menge*; 3 .*Lembah Menge;* 4 . *Boa Leza;* 5 .*Wolo Sege*;6. *Ola Bula*; 7. *Tangi Talo*; 8. *Wolo Mil*o; 9. *Malahum*a; 10. *Wolo Keo*; 11. *Ngamapa*; 12. *Dozu Dhalu*; 13.*Sagala*; 14.*Pauphadh*i; *Deko Weko*

Sources : Suminto, et al., 2009

Figure 4. Stratigraphic section of the Soa showing lithological units and their successions

Figure 5. Chemical reaction of $CaCO_3$ in caliche and tuffaceous limestone of Gero Member, Ola Bula Formation

The Ola Bula Formation unconformably overlies the Ola Kile Formation. The basal Ola Bula Formation is the Tuff Member, which is dominated by pyroclastic flows, tephra, reworked pyroclastic deposits, lahar deposit, fluvial sandstones, and lacustrine. The vertebrate fossils were collected from the layer of tuffaceous siltstones, mud supported, well-moderately sorted, pumice dispersed, erosional contact, and contains fossil bones (Lahar deposits). *Varanus komodoensis, Crocodylus* sp., a Geoemydid and the giant tortoise *Megalochelys* remains are collected, and specially *Megalochelys* is so far restricted in Tangi Talo find site (S08° 41' 34,6"– E 121° 05' 44,6"). Tuff Member is overlied by Sandstone Member. The vertebrate fossils and stone tools are distributed in the Sandstone Member of Ola Bula Formation. The finding vertebrate fossil and stonetools have been excavated in Mata Menge (S 08° 41' 53,0" – E 121° 08' 10,6"). The Sandstone Member predominantly fluvial environments, particularly braided channel systems.

Fossil deposits at Mata Menge are 1.6–2.2 m thick and comprise interbedded layers and lenses of tuffaceous siltstone and sandstone and are indicative of a lakeshore setting close to a tributary stream (van den Bergh *et al.*, 2009; Meijer *et al.*, 2015). The vertebrate fossil and artifact bearing layers are bracketed by a maximum age of 0.88 ± 0.07 Ma and a minimum age of 0.75 ± 0.07 Ma (Morwood *et al.*, 1998; O'Sullivan *et al.,* 2001). Some other fossil sites are Dozo Dhalu (S 08° 42' 23,6" – E 121° 09' 29,7") and Kobatuwa (S 08° 41' 15,5" – E 121° 05' 02,5"). The crocodile fossil was found in the Kobatuwa that preserved in the conglomerate, clast supported, poorly sorted, coarse sand matrix, composed of basalt and andesite fragments, pebble to cobble sized.

Upper most part of the Ola Bula Formation is the Limestone Gero Member, which is white, alternating with fine sandstone, tuff and calcareous tuff. In this period, a climatic change happened abrupt, reflected by a transition from fluvial to a lacustrine environment (Setiawan, 2014). The Limestone Gero Member of the Ola Bula Formation is a limestone formed in a freshwater environment (Figure 5). The Gero Limestone process is as follows: hydrothermy altered volcanic rocks, containing lots of calcium oxide (CaO), as one of the major oxides in the plagioclase feldspar mineral, pyroxene and silicate material of volcanic glass. During the process of weathering and dissolution, $CaO + CO_2$ -- $CaCO_3$ is formed in the form of caliches and calcareous tuff. In the process of dissolving, water (H_2O) evaporates more quickly, because of the Soa area is very dry. As a result, a solution of $CaCO_3$ stays behind and settles on the surface or inserts into the volcanic rock. Caliches are formed together with black mudstone on dry clay and chapped (*Bronto, 2015 pers. comm.*). Above this Gero limestone, unconformably overlies a sediment of a young volcanic alluvial, characterized by andesitic and basalt.

PALEONTOLOGY

Vertebrate fossils are widespread in several sites of Soa Basin, among others: in Kobatuwa, Mata Menge, Lembah Menge, Boa Leza, Ola Bula, Tangi Talo, Wolo Milo, Wolo Keo, Sagala, Dozo dhalu, Kopo Watu, Ngamapa and Paupadhi (Figure 3). They were found in the tuffaceous sandstone member of the Ola Bula Formation (Aziz, *et al.*, 2009). The fossil reptiles are very few and limited, consisting only of a giant tortoise (*Megalochelys* sp.), a crocodile (*Crocodylus* sp.) and the
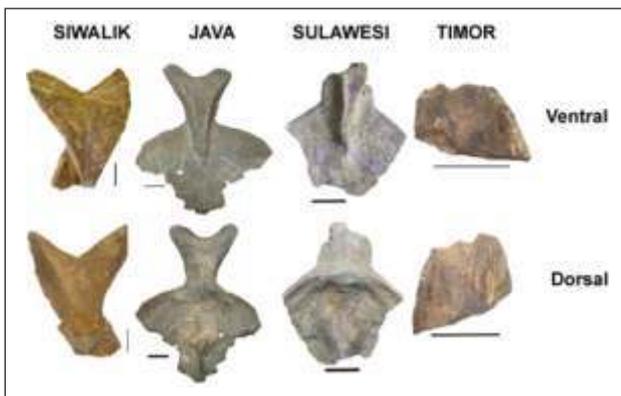
Figure 6. Various forms of anterior plastron (Epiplastron) of *Megalochelys* sp. : Siwalik Hills (India) and Indonesia (Bumiayu Java, Wallanae Sulawesi and Atambua Timor). Scale bars are 10cm.

Figure 7. An assemblage of fragments from one individual of *Megalochelys* sp. (Tangi Talo, Trench G, 2012; a. *carapace* fragment, b. *entoplastron* fragment, c. *scapula,* d. *femur,* e. *nuchal* fragment and f. *scapula*).

komodo (*Varanus komodoensis*) as well as a possibly fresh water turtle (*Geoemydidae*). The reptile fossils are only found in Tangi Talo, Mata Menge, Dozo dhalu and Kobatuwa.

Biostratigraphy of Fauna Unit based on assemblages vertebrate fossils can be classified into two fauna units:

1. The oldest, Tangi Talo Fauna Unit, it is characterized by existence of pygmy Stegodon (*Stegodon sondaari*) and giant land turtle (*Megalochelys* sp.), it is about 1.000.000 years ago or more earlier.

2. The youngest, Mata Menge Fauna Unit, it is characterized by *Stegodon florensis* and stone tools 800.000 years ago.

Overall, the collection of fossils shows clearly an unbalanced endemic island fauna (Simpson, 1965; Dermitzakis and Sondaar, 1979).

Systematic

Class Reptilia Laurenti, 1768
Order Testudines Linnaeus, 1758
Family Testudinidae Batsch, 1788
Genus *Megalochelys* Falconer and Cautley, 1837
Species *Megalochelys* sp.

Giant Tortoise

So far, the specimens of *Megalochelys* from the Soa Basin were only found in the excavations of Tangi Talo, in the sandy tuff layer, which is the lower Tuff Member of the Ola Bula Formation. The layer is about ±40cm thick. Based on anterior epiplastron (Figure 6), we found 8 individuals, however no shell completely conditions from several trenches. In Trench G of Tangi Talo (2012) a collection of shell fragments (carapace and plastron) and

other parts of the skeleton from one individual of *Megalochelys* sp. were found (Figure 7). It could be reconstructed specimen that has 140cm long, it is considered gigantic size for land turtle (tortoise). The extinct giant tortoise genus *Megalochelys,* which was coming from the Siwaliks, the foothills of the Himalaya (India, Asia). It had also found in Irrawady Hill that associated with terrestrial mammals such as Stegodon, suggesting that the age of the fossil bearing beds are attributed to the late Miocene to the early Pliocene (Hirayama, *et al.*, 2015). Furthermore, *Megalochelys* had successfully migrated to the Indonesian Archipelago. Their ability crossed sea water barrier for giant tortoise and distributed to other islands, it should be thought by sea current pattern with floating or rafting (Gerlach, *et al.,* 2006), however the tortoise cannot swim, but it likes to stand in fresh-water pools. The remnants of their presence, in the form of fossils, are found in the Indonesian islands such as Java, Sulawesi, Flores, Timor and Sumba (Hooijer, 1948, 1971; Sondaar, 1981; Aziz, 1994; Setiyabudi 2009b; Setiyabudi, *et al.,* 2012). We consider dispersal events related with sea current pattern towards islands formation within Wallacea region, indicates an intimate association with geophysical aspects of the environment. Based on across the islands, and using lineages endemic to a relatively recent environment, which inferences of long-distance colonization.

The genus name *Geochelone* tends to be used widely (*sensu lato*) for various species of tortoises, whereas the taxonomy was not clear. This is now revised and clarified (Gerlach, 2001; Le, *et al.*, 2006).

Geochelone will be used only for the type specimen of *Geochelone elegans* from India.
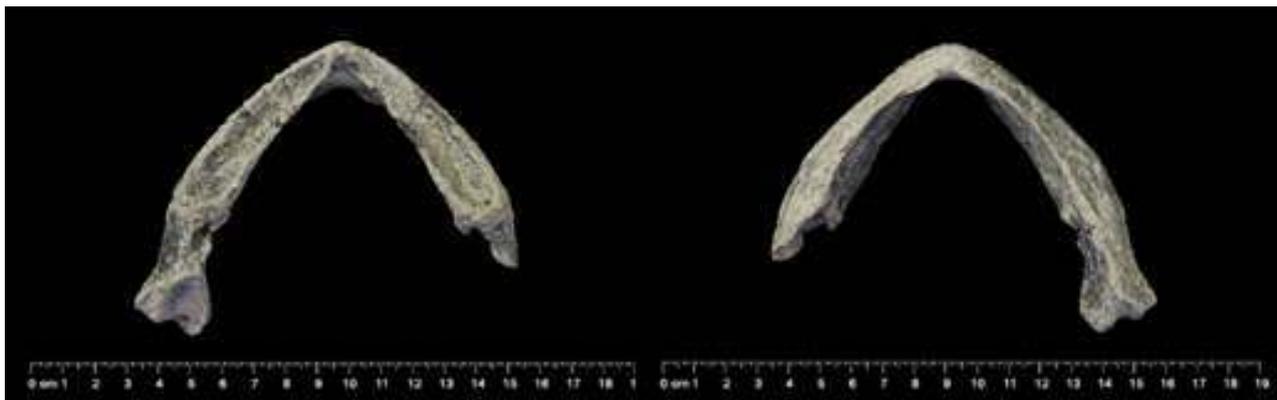
Figure 8. The mandible of *Megalochelys* sp. Tangi Talo excavation 2012 in the Trench G (a. dorsal and b. ventral views). Scale in cm.

Taxonomists have classified the rest of the tortoises into different genera, the name *Geochelone* is no longer widely used (Gerlach, 2001). The genus *Megalochelys* is a giant tortoise up to 2m; the anterior epiplastron is prominent and elongated and branched off at the tips; at the bottom side (inner ventral) of the epiplastron there are indentations (not excavated); the outside form of the epiplastron (outer ventral) is square ridge/flat. These morphological characters are not present in the Genus *Geochelone*. The morphology of the anterior plastron (epiplastron) of the specimens from the Indonesian Islands (Java, Sulawesi, Timor and Flores) as well as the size of a very large shell, are similar to *Megalochelys sivalensis* of the Siwaliks (India) (Falconer and Cautley, 1837; Setiyabudi, 2009a,b). Therefore, the giant tortoises from the Indonesia Islands are classified as *Megalochelys* sp.

Mandible

A mandible of the giant tortoise *Megalochelys* was found during the excavation of 2012 (Figure 8). It got the field number TT G-2012/578 (Tangi Talo Trench G 2012/Fossil no. 578). So far, the mandible is the only specimen found in the Indonesian Islands. The mandible is very important for determination of the tortoise in more detail.

It is a well fossilized specimen and almost complete. It is dark gray colored; only the back of the right side of the condylus portion is missing. The mandible is V-shaped in dorsal and ventral view, as well as trilateral formed, with the front (simphysis) forming an angle of about 75°. The size of the mandible is 104,18mm in length, 120,37mm in width, and the ramus is 19,6mm thick; the condylus has a width of 23,3mm and a height (ramus) of 25,1mm. The giant tortoise multiplies in suitable environment such as dry climate that closed to equator region and a rich water resource for drinking.

Figure 9. Reconstruction of *Megalochelys* sp. Tangi Talo, Flores. Scale bar is 10cm.

This peculiar nasal arrangement is thought to be an adaptation to the dry climate of oceanic islands, allowing the tortoises to drink from very shallow pools of water (Arnold, 1979).

Carapace

The result of the excavations in the Soa Basin has delivered only one top shell (carapace) at Tangi Talo (Figure 9). The average thickness at the center (*vertebral carapace*) of *Megalochelys* from Tangi Talo is about 5mm and the edges (*marginal carapace*) is 20mm, thinner than the species *Megalochelys* from Java, Sulawesi, and Timor, which have a thickness of vertebral carapace average of about 15 - 20mm and a length of about 1.5m - 1.8m. However, *Megalochelys sivalensis* from the Siwaliks (India) can reach a length of 2 meter. The difference in length of the Tangi Talo specimen can be explained by immaturity and a thin shell of the specimen, a size variation within the species or an adaptation to the local environment.
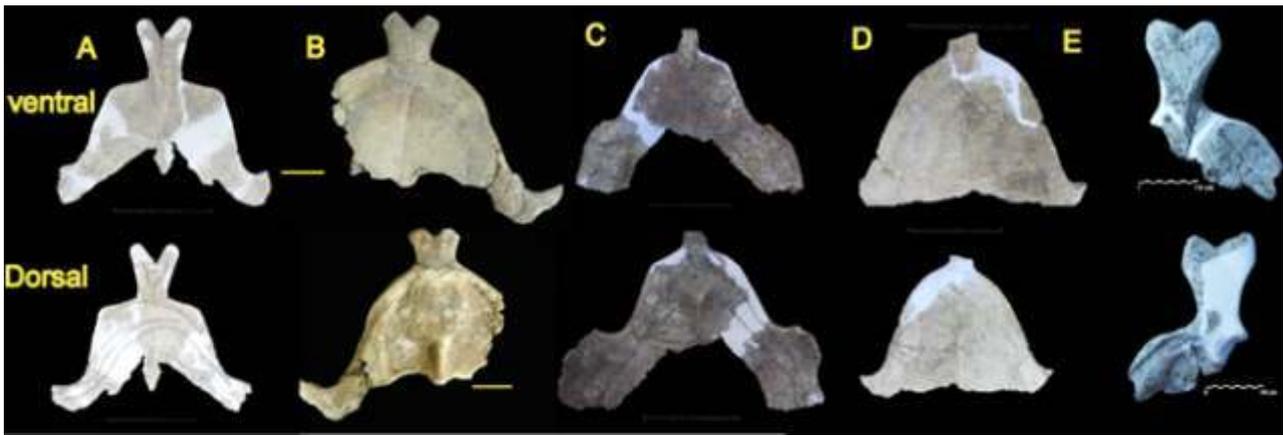
Figure 10. Male type of *Megalochelys* sp. Tangi Talo, Flores. Scale bars are 10cm.
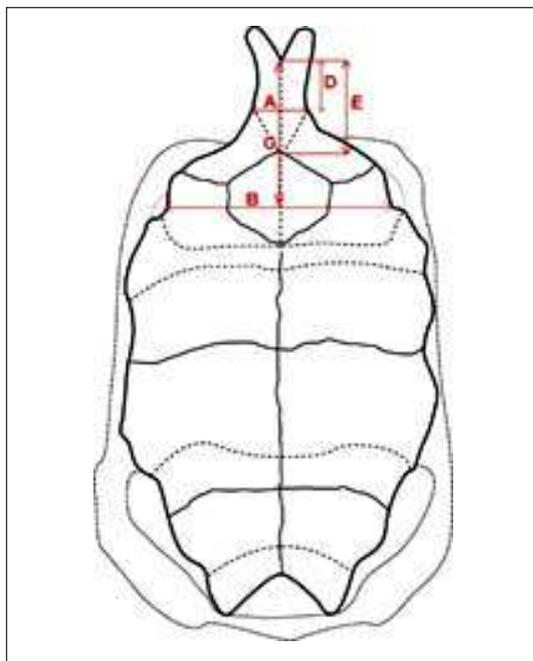
Sources : terminology based on Zingerl, 1969

Figure 11. Scheme of taken measurements of the anterior epiplastron of *Megalochelys*

Epiplastron (anterior plastron)

The Epiplastron is a very important part to determine the sex of a *Megalochelys* sp. Male specimens are characterized by an elongated and branched, concave plastron. Whereas at females the epiplastron is usually rather short, without a bifurcation and the morphology of the plastron is flat. Based on the epiplastron characteristics, all specimens excavated from the tuff layer horizon in Tangi Talo seem to be male individuals (Figures 10 & 11). So far, we cannot recognize more objective for fragmentary materials within female individuals.

Figure 12. The Scapula and the coracoid fan TT G, 2012/633. Scale bar is 10cm

Scapula

The shoulder girdle of *Megalochelys* consists of the scapula and the coracoid fan (Figure 12). The coracoid wide fan is a characteristic part for the species of the tortoise Family Testudinidae. During the excavations at Tangi Talo specimens of the shoulder blade (scapula) of four individuals had been found; one of them (TT G, 2012/633) is almost intact. According to Hooijer (1954) the carapace of the Sulawesian specimen has a length of 20-22 times the length of the scapula. Based on this, it can be estimated that the average length of the *Megalochelys* sp. from Tangi Talo is less than 1.5 m, which means smaller than the specimens from other regions in Indonesia and the Siwaliks. Angle between body scapula and acromium process belonging (Figure 13) Flores specimens is considered more than 90° (110°-120°), which is belonging to tortoise. It has a robust on feet adapted rather than swimming behavior as fresh water turtle. The angle of scapula reflects the shell dome shaped.
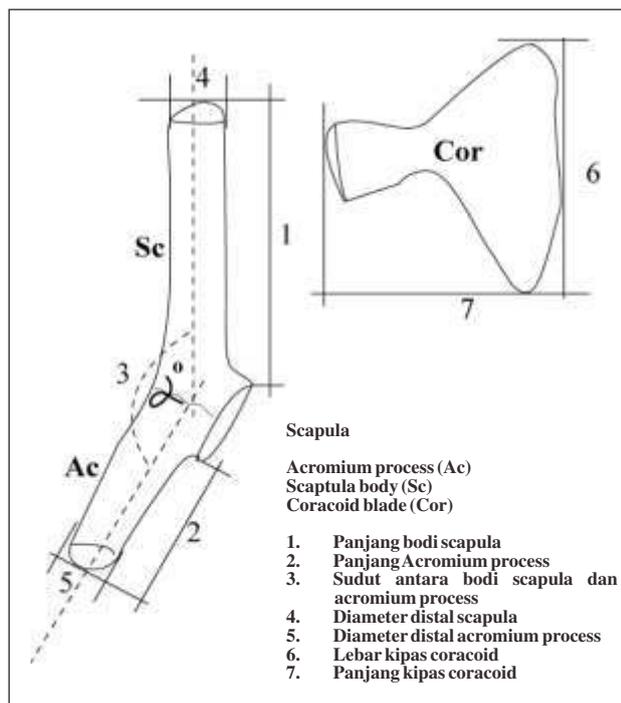
Figure 13. Scheme of measurements of the scapula.

Figure 14. The humeri TT 1991/4066 and TT 1991/4088 of *Megalochelys* (ventral view). Scale bars are 5cm
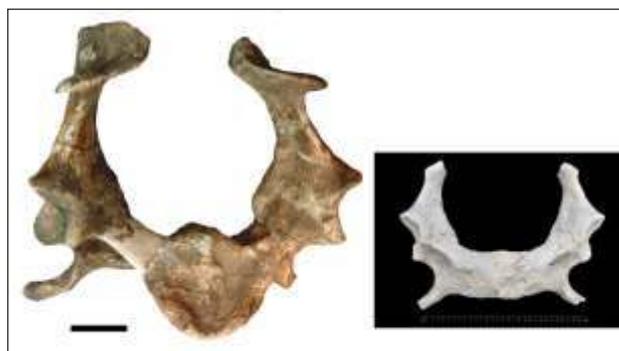
Figure 15. Posterior view of the pelvis: *Megalochelys* from Bumiayu, Java (A) and TT G 2012/32 (B). Scale bar is 10cm.

Humerus

Fossil humeri is rare. Only two specimens (TT1991/4066 [left] and TT 1991/4088 [right] of Trench A) were found in 1991 (Figure 14). Both are not complete and miss the proximal and distal parts. The shape of the humerus is sturdy and short. Specimen 4066 TT has a length of 232,2mm; a cross-section diameter at the proximal humerus of 56.22mm, distal 54.36mm and at the stem (shaft) 56,18mm. Specimen TT 4088 has a length of 174mm, with a proximal diameter of 58.90mm, distal 55.89mm and a stem of about 57.68mm. These humeri shapes are considered incomplete posture. The shape of forelimb is designed a solid undercarriage for weight body of the shell. That is for support rather than for velocity of motion.

Pelvis

Quite a lot of fossil collarbones (pelvis) are discovered at Tangi Talo. However, they are not intact. Only one side, the left or right part are preserved. Specimens TT G/2012/32 is a well preserved specimen (Figure 15). In anterior view, the shaft (illium) of specimen (TT G/2012/32) is perpendicular to the sacral rib, in direct contact with the ribs to the spine section of the carapace. Ischium continued somewhat flat with the pubis. In posterior view, the pubis looks perpendicular and almost rectangular. In contrast to the specimen of Bumiayu (Java) the Illium seems almost a circle and the pubis almost spherical. Based on this, the form of the pelvis can be reconstructed. The overall shape of the carapace from Tangi Talo is smaller and somewhat depressed, while the specimen of Bumiayu (Java) is larger and more convex (dome shaped). However, the shell form can be seen from the pelvic girdle, its part depend on the angle of scapula, where Flores specimen is rather dome shell and anterior aperture shows freely a stick outward of the head.

Femur

Some femora from *Megalochelys* sp. were collected in a number of excavations at Tangi Talo. Reconstructions of several specimens of the femur TT 1991/3886C (trench A); TT 1991/3841 (trench A); TT G 2012/781 (Figure 16) and TT L 2014/179 show a significant morphology. TT1991/3886C and TT1991/3841 were found in trench A in 1991 and are considered to be a pair of thigh bones from the same individual.

Figure 16. Femur TT G/2012/781. In dorsal (left), ventral (center) and lateral (right) views. Scale bars are 10cm

Tabel 1. Assemblages of fossil Reptiles of the Soa Basin

Locality	Taxon	Element
Tangi Talo	*Megalochelys*	Mandible (1) Pelvis (12) Scapula (15) Femur (4) Humerus (2) Tibia (2) Ulna (2) Radius (1) Cervical (5) Carapace (many fragments) Plastron (many fragments)
	Varanus	Humerus (1) Vertebrae (32) Caudal (3) Cervical (1)
	Crocodylus	Teeth (9)
Mata Menge	*Varanus*	Mandible (1) Parietal (1) Maxilla (2) Teeth (30) Vertebrae (10) Phalange (1) Metacarpal/Metatarsal (4) Caudal (4), Vertebra (8)
	Crocodylus	Mandible Teeth (337), Dermal plate (2) Metacarpal/Metatarsal (4) Humerus (1)
Koba Tuwa	*Varanus*	Vertebra (2) Bone fragment (1)
	Crocodylus	Cranium (1) Mandible (3) Teeth (5) Vertebra (1) Femur (1)
Dhozo Dhalu	*Varanus*	Tooth (1)

However, TT1991/3841 is dark brown in color compared to TT1991/3886C, which was found intact at the distal fracture, but missing such a long part. It is impossible to make accurate measurements (Table 3). The femur found in trench G during 2012 is registered as TT G 2012/78. The femur is light brown in color. The specimen is intact, although there are cracks and it is broken at the distal part. The dimensions of the femur are relatively similar to those of the specimens found in trench A, but the specimen is considered to be more mature, than the one discovered in 1991. TT L 2014/179 is a femur which was found in the silty tuff horizon of Tangi Talo in trench L. It is of light brown color. It was found intact, although the proximal part of the trochanter is a little broken, slightly behind the femur head, because of the fragility. This femur is the longest femur compared to the previously discovered ones in this horizon (Table 3)(Figure 17).

Systematic
Class Reptilia Laurenti, 1768
Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Family Geoemydidae Theobald 1868
Genus *Cuora* Gray, 1856
Species *Cuora amboinensis* Gray, 1856

The fresh water turtle (?*Cuora amboinensis*)

Besides specimens of Megalochelys, collected in Tangi Talo (2014), also a pelvis was found (Figure 18), which is very small (± 5cm) and further a marginal carapace fragment (size 30mm x 40mm), which both seem not to be of Megalochelys. The plate of the hyoplastron portion (buttress) penetrates into the ribs and limit the outskirts of a line plastron bulge (ridge). This is a character of the freshwater turtle (?) *Cuora amboinensis* (*Takahashi,2015 pers. comm.*). Furthermore, we still need more data and additional specimens to come to a final conclusion.

Table 2. Measurements of the anterior epiplastron of *Megalochelys* sp. of Tangi Talo, Flores.

No Specimen	Year	Measurements (mm)					Estimation of maximum size			
							Plastron(cm)		Carapace(cm)	
		A	B	C	D	E	Lenght	Width	length	width
TT-I/96	2014	74,44	-	-	146,86	208,28	-	-	-	-
TT-I/6	2014	95,55	510,0	420,0	106,21	240,0	-	-	-	-
TT-H/13	2014	86,26	530,0	420,0	37,66	166,56	?	?	?	?
TT-H/33	2014	108,99	550,0	530,0	198,12	270,0	-	-	-	-
TT-A/4290	1991	106,78	500,0	430,0	117,51	200,0	-	-	-	-
TT-G	2012	131,50	580,0	450,0	125,97	260,0	120	96	139	104

Table 3. Measurements of the scapulae of *Megalochelys* species

No. Spesimen	Locality	Measurement (mm)						
		1	2	3	4	5	6	7
TT A 4084/1991	Tangi Talo	240.6	140.2	107	44.8	41.3	-	-
TT A 4280/1991	Tangi Talo	250.5	147.4	108	40.7	36.1	-	-
TT A 3849/1991	Tangi Talo	-	-	-	-	-	128.0	116.6
TT A 3854/1991	Tangi Talo	144.4	109	108	33.4	37.5	-	-
TT G 2012/829	Tangi Talo	183.9	120.3	110	39.5	43.69	-	-
TT G 2012/810	Tangi Talo	230.2	125.8	110	31.7	30.1	-	-
TT G 2012/631	Tangi Talo	230.8	115.3	110	30.7	22.7	-	-
TT G 2012/633	Tangi Talo	230.5	113.2	110	41.6	25.5	-	-
TT G 2012/837	Tangi Talo	-	-	-	-	-	109.7	149.5
TT G 2012/654	Tangi Talo	-	-	-	-	-	108.6	148.3
TT K 2014/23	Tangi Talo	228.2		109	41.1	38.0	-	-
TT K 2014/5	Tangi Talo	-	-	-	-	-	100.6	172.9
RMNH, Leiden NL	Wallanae, Sulawesi	233	30.21	120	38.33	12.44	-	-
SB 1989	Wallanae, Sulawesi	320	222	110	33.90	29.89	-	-
Timor (*unregistered*)	Atambua, Timor	221	71.33	110	14.33	14.19	-	-

Scapula
1. Length of the body scapula
2. Lenght of acromium process
3. Angle between body scapula and acromium process

4. Diameter of distal scapula
5. Diameter of distal acromium process
6. Width of coracoid fan
7. Lenght of coracoid fan
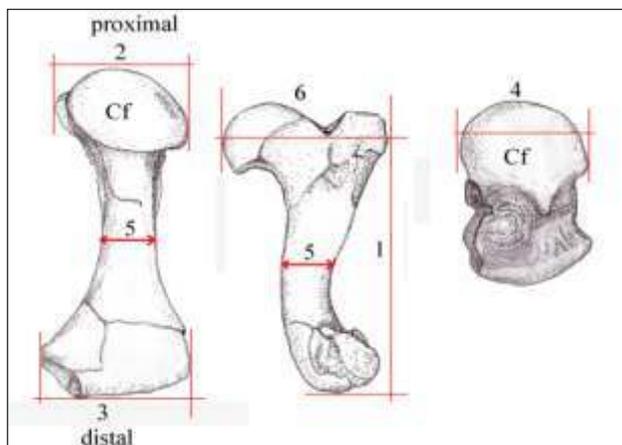
Source : setiyabudi, 2009

Figure 17. Scheme of the measurements of the femur. Cf = Caput femoralis

It is justified that the existence of fresh water turtle is likely closed to river habitats that give multiply and diversity in the Tangi Talo area in the past.

Systematic

Class Reptilia Laurenti, 1768
Order Crocodylia Gmelin, 1789
Family Crocodylidae Laurenti, 1768
Genus *Crocodylus* Laurenti, 1768
Species *Crocodylus siamensis* Schneider, 1801

Figure   18. The Pelvis from the fresh water turtle ?*Cuora amboinensis*, TT H-b 2014/46

Table 4. Measurements of the femura.

Fossil specimens	1	2	3	4	5	6
TT A 1991/3841	214.0	67.30	-	64.03	35.91 x 37.81	120.6
TT A 1991/3886C	200.0	67.01	87.31	73.42	33.87 x 29.27	106.2
TT G 2012/781	233.5	86.12	96.57	75.60	34.45 x 41.76	116.9
TT L 2014/179	258.3	119.3	111.7	77.46	35.61 x 43.76	124.7

Femur
1. Lenght of femur shaft
2. Width of proximal head
3. Width of distal head

4. Width of proximal head
5. Diameter of middle part of femur shaft
6. Thick of femur head
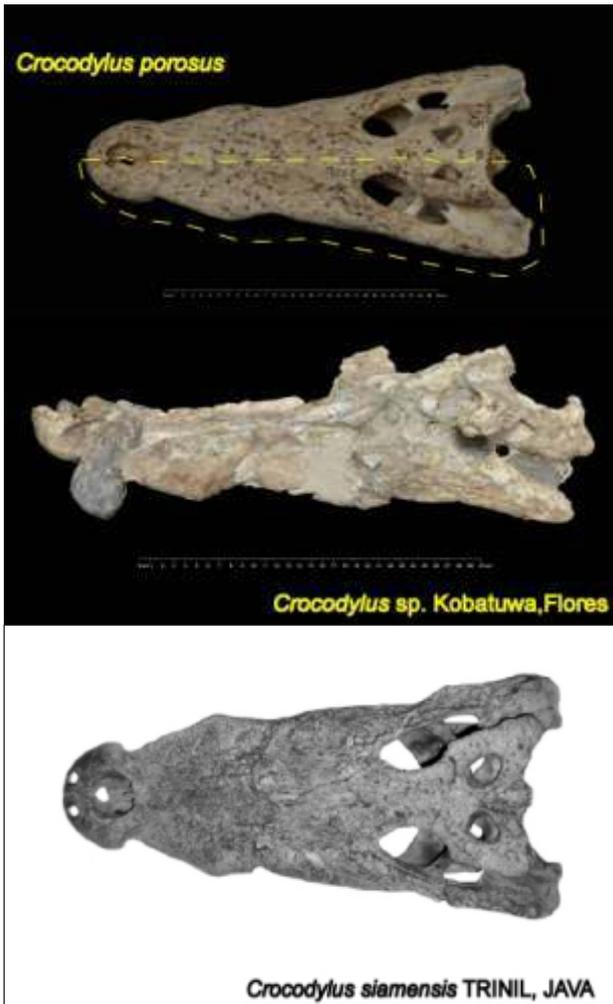
Source : modified from Delfino and de Vos, 2010

Figure 19. Comparative left skull of *Crocodylus porosus* and *Crocodylus* sp. from Kobatuwa,   and *Crocodylus siamensis* from Java

Figure 20. The Right Mandible *Crocodylus* sp. Kobatua, Soa Basin.

Figure 21. The right femur of *Crocodylus* sp. from Mata Menge 2012 (MM 31 2012/452).

Crocodyle

A few specimens of fossil crocodiles (*Crocodylus* sp.) have also been found in the Soa Basin of Mata Menge, Kobatuwa and Tangi Talo, although in limited quantities. Specimens were found, among others, in the form of isolated teeth, femur and skull fragments. Isolated teeth are most commonly found at Mata Menge and Tangi Talo. Fossil teeth of the site of Mata Menge and Tangi Talo shows a variation in size and conical morphology, which is similar in size and shape of crocodile teeth in general. The height of the teeth ranges from 13,58 – 6,11 mm and have a diameter of 27.25mm to 13.84mm. The Femur MM 2012/452 from Trench 31, found during the excavations of Mata Menge (2012) is cylindrical in shape, with a length of 214.3mm, proximal width 51.18mm and distal 44.73mm. The dimensions of the femoral shaft in the center are 25.91 x

22.27mm. The shape of the femur is distally curved downwards. In Kobatuwa a right mandible fragment and a left side of a skull fragment were found(Figure 21). These are the only crocodile fossils in that site. They are relatively well preserved, although not intact (Figures 19 and 20). The basal occipital of the skull of the fossil crocodile *Crocodylus* sp. from Kobatuwa is different from the estuarine crocodile *Crocodylus porosus*, which is flatter and not oval, and seems to resemble *Crocodylus siamensis* of Java (Delfino & de Vos, 2010). However, the relative size is the same as the estuarine crocodile *Crocodylus porosus*, which is still living today and has a size less than 500mm, while *Crocodylus siamensis* is greater than 500mm. This difference is possibly related to maturity or age of the individual. The right lower jaw (mandible) of the Kobatuwa crocodile shows morphology similar to *Crocodylus siamensis* of Java.

Figure 22. The right Mandible of the fossil Komodo from Mata Menge.

Systematic

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Family Varanidae Gray, 1827
Genus *Varanus* White, 1790
Species *Varanus komodoensis* Ouwens, 1912

Varanus komodoensis

Varanus komodoensis is the remnant of an ancient fauna, which has a close relationship with the Pleistocene giant lizard of Australia *Megalania* sp. It measures up to 8 meters (Hocknull, *et al.,* 2009). Based on the hypothesis that the oldest varanid fossils are of the Early Cretaceous, about 95 million years ago, in Europe and Asia, and there is going on a dispersal and radiation since the Cretaceous, there must be a kinship of Indo Asia and Indo Australia (Molnar & Pianka,

2004). Today, *Varanus komodoensis* is only living in islands of Rinca and Komodo. At its arrival, about 2 million years ago, it must have had already a large body size (Hocknull, *et al.,* 2009). In addition to Flores, Komodo fossils were also found in Sulawesi, Sumba and Timor of the Walacea Islands (Brongersma, 1958; Hooijer, 1972; Setiyabudi, *et al.,* 2012). The Komodo dragon fossils found in Mata Menge consist of isolated teeth, a right lower jaw fragment (mandible) and a piece of the back of the skull (parietal) (Figures 22 & 23). While in Tangi Talo and Dozo Dhalu only isolated teeth were found. The isolated teeth with roots are conical shaped, relatively flat and serrated from the stem to the tip. The right lower mandible (MM T.30 2012/14) from Mata Menge has a length of 111.36mm, a width of the ramus of 33.23 -19.15mm.It is relatively intact with a few teeth still in place. The parietal (MM T.21 2011/28) found at Mata Menge is similar in morphology with the Komodo dragon *Varanus komodoensis,* that is still living today (Figure 23).

DISCUSSION

Despite of the regression of the sea level, islands of Wallacea were never connected to the Asian mainland (Sunda Shelf) and Australian mainland (Sahul Shelf). The Asian mainland fauna has, in order to reach Flores, to cross a sea barrier. This is not a significant barrier for some native Asian mainland taxa, such as the proboscidean *Stegodon.*

Figure 23. The parietalis of the fossil Komodo of Mata Menge.

Source : Kuhnt, et al., 2004
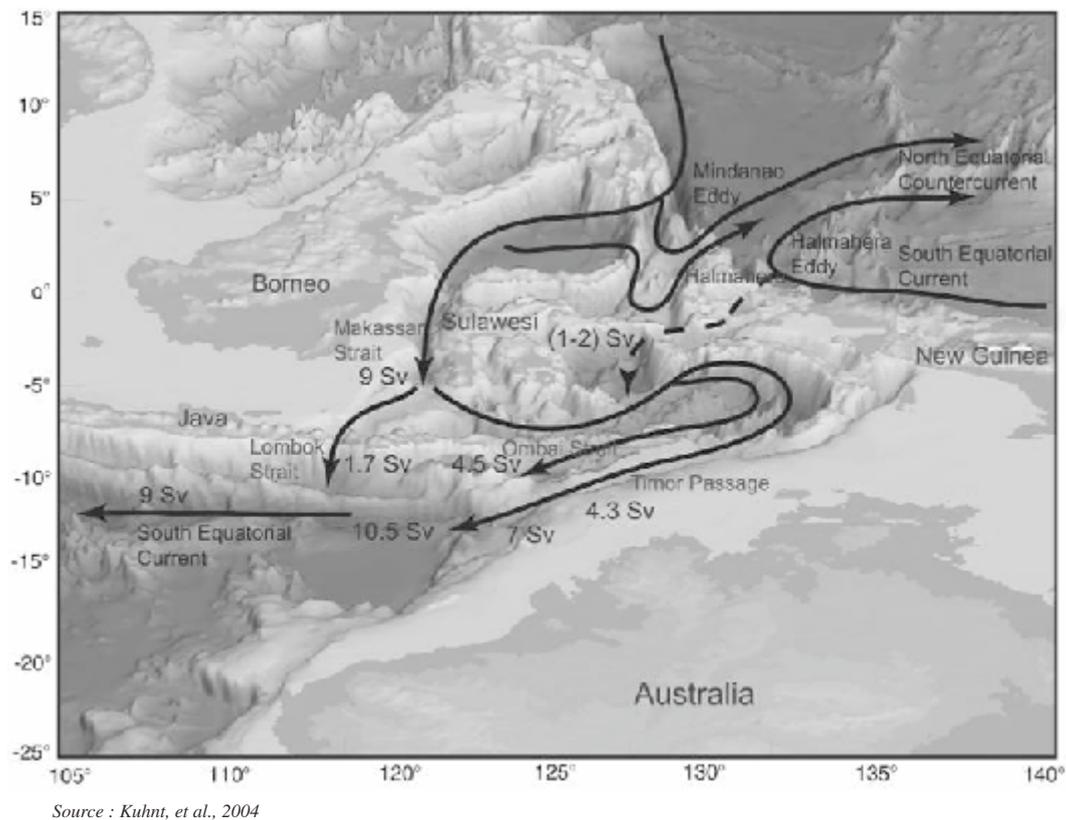
Figure 24. Throughflow of Indonesian sea current

This is also true for the tortoise (*Megalochelys* sp.), the Komodo dragon (*Varanus komodoensis*) and the crocodile (*Crocodylus* sp.). *Megalochelys* can cross a sea barrier, because of the shape of its body, which can make them float in the sea and further they can survive without food and drinks for several days (Arnold, 1979). *Crocodilus* has a gland organ, with which it can adapt to salt water, so that it can migrate between islands (Taplin & Grigg, 1989) and probably this is also true for the Komodo dragon (*Varanus komodoensis*). They came to Flores by swimming or floating and settled in the Soa Basin. This kind of dispersal is known as sweepstake dispersal (Simpson, 1965; Dermitzakis and Sondaar, 1979). To reach Flores from the Asia Continent (Java) the taxa must be at least capable of crossing the Lombok Strait (width 25km) and Sape Strait (10km wide) which is difficult. Besides this, one must also take in account the local patterns of currents and wind, which have been influent by the Indonesian Throughflow (Kuhnt, *et al*., 2004) (Figure 24). The sea current direction is from the north to the south that winding up via the Lesser Sunda passages and the end in the Hindia Ocean. Based on the above and take in account at the fauna composition, which is more diverse in Java (a balanced fauna), than the fauna of the

Philippines, Sangihe, Betue, Wallanae and Flores, which are of the unbalanced endemic island fauna type, then the migration path from Asia to Flores is more likely via the Philippines, Sangihe and Sulawesi, as proposed by Aziz (2008). Isotope analysis in *Stegodon* teeth of Tangi Talo showed that their diet was dominated by leafs, indicating again a wet environment (humid), while the *Stegodon* from Mata Menge had a more grassy diet, which shows a dry environment (Puspaningrum, *et al.,* 2014). Based on pollen analysis the fossil fauna in the Soa Basin adapted to a dry environment like a savannah, a bit rainy, humid, and the temperature was very high (Polhoupessy, 2001).

Keep in mind that Mata Menge is located relatively further away from the river Ae Sissa, compared to Tangi Talo. Presumably there was less rain around Mata Menge, becoming more dry, so that the plants which were growing there were dominantly grasses, while the area surrounding Tangi Talo, closer to the river Ae Sissa, was more humid, which resulted in more foliage. Additional we can state that the proboscidean (*Stegodon* sp.) was more in a water environment. This we find back in the giant tortoise (*Megalochelys* sp.), the Komodo dragon (*Varanus* sp.), fresh water turtle Geoemydid and the crocodile (*Crocodylus* sp.). Overall the Soa Basin

fauna lived in a savannah environment close to water sources of the Ae Sissa River or maybe in a lake or swampy area.

CONCLUSION

The Wallace' Line is not the boundary line to the east for the dispersal of some animals of the Asian mainland. Not only the *Stegodon* sp., but also some reptiles from the mainland of Asia, like the giant tortoise (*Megalochelys* sp.), the komodo dragon (*Varanus komodoensis*), freshwater turtle (?*Cuora amboinensis*) and a crocodile (*Crocodylus siamensis*) could cross Wallace's line by swimming or floating via "*sweepstake dispersal*" (Simpson, 1965; Dermitzakis and Sondaar, 1979). They came to Flores about 1 million years ago or earlier via the northern route: Mainland Asia via Taiwan - Philippines (Luzon) - Sangihe (Pintareng) - Sulawesi (Betue - Wallanae) to East Nusa Tenggara (Flores-Sumba and Timor) as suggested by Aziz (2008). The *Megalochelys* sp. from the Soa Basin is slightly smaller (carapace length of 1.37m with a carapace thickness <5mm) in comparison with those found in Java, Sulawesi, Sumba and Timor (carapace length of 1.5 - 1.8 m with a thickness of up to 20mm carapace). Further study is needed to know with certainty the differences between the species. Whether the specimens of Tangi Talo are of an immature individual or another species/subspecies or an adaptation to the local environment has to be worked out. The *Crocodylus siamensis* and *Varanus komodoensis* show a similar morphology to the living ones. Similar with the Freshwater Turtle (?) *Cuora amboinensis*, which shows resemblances in morphology to the species that still lives today. May be the variation in the population is the result of adaptation to the local environment or a local evolution. The fauna assemblage of the Soa Basin indicates an unbalanced endemic island fauna, living in a savannah environment, close to the stream Ae Sissa or maybe a lake or a swamp.

ACKNOWLEDGEMENT

REFERENCES

Arnold, E.N., 1979.   Indian Ocean giant Tortoises: their systematics and island adaptations. *Philosophical Transactions of the Royal Society, London B*, vol. 286, p. 127-145.

Aziz, F., 1990. Pleistocene mammal faunas of Sulawesi and their bearings to paleozoogeography, Dissertation, Kyoto University, 106pp.

Aziz, F., 1994.Vertebrate faunal evolution of Sulawesi Island, Indonesia during Late Neogene. In: R. Tsuchi (Eds) *Pacific Neogene Event in Time and Space*, IGCP – 246, p.79 – 85.

Aziz, F. 2000. The Pleistocene Endemic Fauna of the Indonesian Archipelago. *Tropics,* 10 (1), p. 135-143.

Aziz, F. 2008. Evolusi Dan Paleontologi Vertebrata Indonesia: Prespektif Perubahan Iklim. *Orasi Pengukuhan Profesor Riset. Badan Geologi*, Departemen Energi Dan Sumber Daya Mineral, 76pp.

Aziz, F., M.J. Morwood & van den Bergh G.D., 2009. Pleistocene Geology, Palaeontology and Archaeology of the Soa Basin, Central Flores, Indonesia. *Geological Survey Institute Bandung, Indonesia, Special Publication,* 36, 146pp.

Brongersma, L.D., 1958. On an extinct species of the Genus Varanus (Reptilia, Sauria) from the island of Flores. *Zoologische Mededelingen Museum Leiden*, 36(7), p.445-447.

Conrad J.L. (2008). Phylogeny and Systematics of Squamata (Reptilia) Based on Morphology. *Bulletin of the American Museum of Natural History, Number 310*, New York. 182pp.

Delfino M. and de Vos, J. (2010). A Revision of the Dubois Crocodylians, Gavialis Bengawanicus and Crocodylus ossifragus, from the Pleistocene Homo Erectus Beds of Java. *Journal of Vertebrate Paleontology, 30(2),* p. 427–441.

Dermitzakis, M.D. and Sondaar, P.Y. 1979. The importance of fossil mammals in recontruction paleogeography with special reference to the Pleistocene Agean Archipelago. *Ann. Geol. Hellen. Athenes, 46, p*.808- 840.

Ehrat, H. 1925. Geologische Mijinbouwkundige onderzoekingen op Flores, *Jaarboek v.h. Mijinwezen in N.O.1 Verhandelingen Geologische Schetskaart* 250,000.

Falconer, H. & Cautley, P., 1837. On additional fossil species of the order Quadrumana from the Siwalik Hills. *Jour. Asiatic Soc. Bengal,* vol. 6, p.354-360.

Gerlach, J., 2001. Tortoise phylogeny and the 'Geochelone' problem. *Phelsuma* vol. 9 (supplement A), p.1-24.

Gerlach, J., Muir, C., and Richmond, M.D., 2006. The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History*, 40(41-43), p. 2403-2408.

Grigg, G. and Gans C., 1993. Morphology and physiology of the Crocodylia. In: Glasby, C J Ross G J & Beesley P L (eds), *Fauna of Australia*, Vol. 2A, Amphibia and Reptilia. AGPS,

Canberra. p. 326–336.

Hartono, H.M.S., 1961. Geological investigation at Ola Bula, Flores: Bandung, Indonesia. *Djawatan Geologi,* 40pp.

Hirayama, R., Sonoda, T., Takai, M., Htike, T., Thein, Z.M.M. and Takahashi, A., 2015. Megalochelys: gigantic tortoise from the Neogene of Myanmar. *The 5th Turtle Evolution Symposium, Rio de Janeiro, Brazil*. (doi.org/10.7287/peerj.preprints.961v1).

Hocknull S.A., Piper P.J., van den Bergh G.D., Due R.A., Morwood M.J. & Kurniawan, I., 2009. Dragon's Paradise Lost: Palaeobiogeography, Evolution and Extinction of the Largest-Ever Terrestrial Lizards (Varanidae). *PLoS ONE4* (9) e7241.

Hooijer, D.A., 1948. Pleistocene Vertebrate from Celebes II.Testudo margae nov. spec. *Konikl. Nederl.Akad.van Wetens.-Amsterdam. Reprint.from Proc.*, 60, p.1169-1182.

Hooijer, D.A., 1949. Pleistocene verrehrares from Celebes. IV. Archidiskodon celebensis nov.spec.. *Zool. Meded. Museum Leiden*, 30 (14), p.205-226.

Hooijer, D.A., 1954. Pleistocene Vertebrate from Celebes X. *Konikl. Nederl. Akademie Van Wetenschappen-Amsterdam, reprint from Proc. Series B*, 57 (4), p.486-489.

Hooijer, D.A., 1957. A Stegodon from Flores. *Treubia,* 24, p.119-128.

Hooijer, D.A. (1971). A giant land tortoise, Geochelone atlas (Falconer et Cautlay), from the Pleistocene of Timor. I & II. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, 74, p.504-525.

Hooijer, D.A. 1972. Varanus (Reptilia, Sauria) from the Pleistocene of Timor. *Zoologische Mededelingen Museum Leiden*, 47, p.445-447.

Kuhnt, W., Holbourn, A., Hall, R., Zuvela, M., and Käse, R., 2004.Neogene History of the Indonesian Throughflow, in Continent-Ocean interactions within East Asian Marginal Seas (Eds. Clift, P., Kuhnt, W., Wang, P., and Hayes, D.). *American Geophysical Union, Washington D.C.,* p.1-22.

Le, M., Raxworthy C. J., McCord W. P., & Mertz, L., 2006. A molecular hylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, 40, p.517–531

Maringer, J. and Verhoeven, T., 1970. Die Steinartefakte aus der Stegodon-Fossilschicht von Mengeruda auf Flores, Indonesien. *Anthropos,* 65, p.229-247.

Meijer, H.J.M, Kurniawan, I., Setiabudi, E., Brumm, A., Sutikna, T., Setiawan, R., van den Bergh, G.D., 2015. Avian remains from the Early/Middle Pleistocene of the So'a Basin, central Flores, Indonesia, and their palaeoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 440, p.161–171.

Molnar, E.R. &Pianka, E.R. 2004. Biogeography and Phylogeny of Varanoids. in Pianka, E. R. and King, D.R. (eds.) 2004. *Varanoid Lizards of the World. Indiana University Press, Chapter 3*, p.68-76.

Morwood, M.J., O'Sullivan, P., Aziz, F. & Raza, A. (1998). Fission track age of stone tools and fossils on the east Indonesian island of Flores. *Nature,* 392, p.173–176.

Muraoka, H., Nasution, A., Urai, M., Takahashi, M., And Takashima, I., 2000. Regional Geothermal Geology of The Ngada District, Central Flores, Indonesia. P*roceedings World Geothermal Congress 2000 Kyushu - Tohoku, Japan*, p.1473-1478.

O'Sullivan, P.B., Morwood, M.J., Hobbs, D., Aziz, F., Suminto, Situmorang, M., Raza A. & Maas, R., 2001. Archaeological implications of the geology and chronology of the Soa Basin, Flores, Indonesia. *Geology,* 29(7), p.607–610.

Polhaupessy, A.A.,2001. Vegetation and environment of the Soa Basin Central Flores. *Majalah Geologi Indonesia*, vol.16 (3), p. 135-145.

Puspaningrum, M., van den Bergh, G.D., Chivas, A., Setiabudi, E., Kurniawan, I., Brumm, A., Sutikna, T., 2014. Preliminary results of dietary and environmental reconstructions of Early to Middle Pleistocene Stegodons from the So'a Basin of Flores, Indonesia, based on enamel stable isotope records. *Abstract Book of the VIth International Conference on Mammoths and their Relatives. S.A.S.G.*, *Spec.* Vol. 102, p.164-165.

Sartono, S., 1969. Stegodon timorensis: A pygmy species from Timor. *Koninklijk Neder- lands Akademie van Wetenschappen, Proceedings Series B* 72, p.92-202.

Setiawan, R., 2014. *Geoarcheology of the Soa Basin Indonesia: new consideration on stratigraphy and paleoenvironment.* University of Wollongong, Australian. Dissertation University of Wollongong, Australia.

Setiyabudi, E., 2009a. *Systematic Study on the Early Pleistocene Tortoises from the Indonesian Islands and their Paleozoogeographic Implication.* Dissertation Kagoshima University Japan, 137pp.

Setiyabudi, E., 2009b. An early Pleistocene giant tortoise (Reptilia; Testudines; Testudinidae) from the Bumiayu area, Central Java, Indonesia. *Journal of Fossil Research*, 42(1), p.1–11.

Setiyabudi, E., Kurniawan, I, & van Den Bergh, G.D., 2012. Fossils of *Stegodon* and *Varanus Komodoensis* Sumba and Flores: A Pleistocene Landbridge?. *Prosiding 41st IAGI Annual Convention and Exhibition,* p.618-621.

Simpson,G.G., 1965. *The geography of evolution, collected essays*. Chilton Books, Philadelphia, 249pp.

Sondaar, P.Y.,1981. The *Geochelone* faunas of the Indonesian Archipelago and their paleogeographical and biostratigraphical significance. *Mod. Quat. Res. SEAsia*, 6, p.111-120.

Sondaar, P.Y., 1987. Pleistocene mammals and extinctions of islands endemics. *Mem. Soc. Geol. France* N.S. 150, p.159-165.

Sondaar, P.Y., van den Bergh, G.D., Mubroto, B., Aziz, F., De Vos, J. & Batu, U.L., 1994. Middle Pleistocene faunal turn-over and colonisation of Flores (Indonesia) by *Homoerectus. Comptes Rendues de l'Academiedes Sciences*, 319, p.1255-1262.

Taplin, L.E. and Grigg, G.C., 1989. Historical zoogeography of the eusuchian crocodilians: a physiological perspective. American Zoologist 29, p.885–901.

van den Bergh G.D,Meijer H.J.M, Due Awe R., Szab´o K., van den Hoek Ostende L.W., Sutikna T.,Saptomo E.W., Piper P.J., Dobney K.M.,Morwood M.J. 2009. The Liang Bua faunal remains:a 95 k.yr. sequence from Flores, East Indonesia. *Journal of Human Evolution* 57, p.527–537.

Wallace, A.R., 1863. On the physical geography of the Malay Archipelago. *Journal of the Royal Geographical Society*, 33, p.217-234.

Zangerl, R. 1969. The turtle shell. In: Gans, C. and T. Parsons (eds.), B*iology of the Reptilia, Volume 1*. Academic Press, New York. p. 311–339.