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Suyono

University of Wollongong

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The Study of fossil faunas in the Walanae Basin, Indonesia

*A thesis submitted in fulfillment of the requirement for the
award of the degree*

Master of Science

from

UNIVERSITY OF WOLLONGONG

by

Suyono

GeoQUeST Research Centre

School of Earth and Environmental Sciences

2009

DECLARATION

I, Suyono, declare that this thesis, submitted in fulfilment of the requirements for the award of Master Science, in the School of Earth and Environmental Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Suyono

20th October 2009

Acknowledgment

This study would not have been possible without the assistance of several organisations, including the University of Wollongong (for a University Postgraduate Scholarship), the Australian Research Council (for funding the ‘Astride Wallace’s Line 2’ project), and the Geological Survey of Indonesia (GSI).

Many individuals advised and assisted with the work. Firstly, I would like to express my gratitude to Professor Mike Morwood for creating this opportunity to study at University of Wollongong, as well as support and supervision above and beyond the role of a supervisor; Dr. Gert van den Bergh for discussion, providing, inspiring and encouraging this research; and Dr Kira Westaway (for her support in the field). Dr. Sukhyar (Head of the Geological Agency, Department of Energy and Mineral Resources); Dr. Djadjang Sukarna (Vice-Head of the Geological Agency, Department of Energy and Mineral Resources); Dr. A. Djumharna (Director of GSI), Professor Fachroel Aziz, Dr. Yunus Kusumahbrata and Ir. Eko Edi Susanto also provided generous support for this study.

It is a pleasure to also thank the following individuals: Professor Brian Jones (for the ‘Stratigraphy and sedimentology’ course), Professor Gerald Nanson and Dr. Tim Cohen (for the ‘Geomorphology’ course), Professor Bert Roberts, Professor Alan Chivas and Dr Zenobia Jacobs (for the ‘Dung, death and decay’ Course), and all other staff and student colleagues at the School of Earth and Environmental Sciences. In addition, members of the Wollongong and Doncaster Avenue Indonesian communities helped maintain my level of sanity.

Many other people participated in the Sulawesi fieldwork, including M. Anwar Akib, Slamet Sudjarwadi, Ruli Setiawan, Dida Yurnaldi, Iwan Kurniawan, Dadang and other staff from GSI and the Geological Museum in Bandung. I would also like to thank Mrs. Megumi Kondo and Matsu'ura Sensei for providing me with a notebook computer and other Japanese researchers for discussing aspects of the research. Their contribution is very much appreciated.

Dr Gono gave permission to work on recent suid skull material in the collections of the Museum Zoologicum Bogoriense; Prof Colin Groves allowed me access to recent suid material in the collections of the Australian National University; and the websites www.iucnredlist.org, and <http://chasmosaurine.blogspot.com/2007/02/natural-history-of-pigs-part-ii-tusks.html> were excellent sources of recent suid photos and distribution maps. I thank them all.

Finally, I am truly grateful to my parents, to my wife, Finna Laffany, and to my son Refli Nabil Rabbani for making this long-held dream become a reality, and for their unwavering support and encouragement, without which I could not have completed this thesis.

ABSTRACT

The main purpose of my research was to reconstruct the morphology and phylogenetic history of *Celebochoerus heekereni*, an endemic pig species known from Pliocene fossil deposits in the Walanae Basin of Southwest Sulawesi, Indonesia. An important part of this research was to refine the age range of *C. heekereni* and to reconstruct its paleogeographic context on the basis of Southeast Asian plate tectonics and eustatic sea-level changes. This study has implications for the history of other animal species on Sulawesi, and for Southeast Asian biogeography generally.

Associated fieldwork in the Walanae Basin included the description of fossil sites, the recording of stratigraphic sections, two excavations, and the collection of sediment samples for palaeoenvironmental reconstruction and dating. Associated analyses included qualitative and quantitative morphological analysis of *C. heekereni* cranial and dental remains collected either by previous researchers or during my fieldwork. Comparative data was also obtained on other extant and extinct pigs, including those of the before genus *Sus* and *Babyrousa*. This data was obtained from the published literature, as well as from my analyses of material held in the collections of the Indonesian Geological Survey Institute in Bandung, the Zoological Museum in Bogor, and the Australian National University in Canberra.

Concerning phylogeny, *C. heekereni* shows a combination of primitive and advanced skull characteristics. Comparative analyses indicate that the ancestor of this species was most likely close to *Palaeochoerus*, a primitive suid genus known from the Lower Miocene of the Siwaliks in the Indian subcontinent, which gave rise to various Eurasian and African suid lineages, including extant warthogs. In contrast, dental morphology in *C. heekereni* underwent little change except for a reduction of the anterior premolars and an increase in the size of the upper canines.

A synthesis of the available geological evidence indicates that since the Middle Eocene, no part of Sulawesi has been connected to the Asian mainland. As the ancestor of *C. heekereni* cannot have entered Sulawesi before the Lower Miocene, it had to have crossed a sea barrier. This could have occurred during the Middle

Miocene, when deltaic progradation on the east coast of Borneo extended further east than at present, and crossing the Makassar Strait to reach Sulawesi would have been less difficult.

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CHAPTER ONE

INTRODUCTION

I.1. The Aim of the thesis

The main purpose of my palaeontological research is to reconstruct the age range, environmental context, functional anatomy, phylogeny and behaviour of *Celebochoerus heekereni*; an extinct pig species known from fossil remains in Southwest Sulawesi, Indonesia.

Palaeontology is the major source of information on past faunal dispersals, evolution and extinctions, in the context of climate change and human impacts. The history of *Celebochoerus heekereni* - how and when the associated suid lineage reached Sulawesi; how it evolved over time; and when and why it became extinct, should provide insights into the history of other endemic species on the island, including hominins.

In turn the faunal sequences on Sulawesi, and the determinants of change there, provide a case study with general implications for the faunal history of Southeast Asia generally. This information is relevant to meeting some of the major conservation challenges in the region. Hopefully, some of the data generated in my study will prove of such value.

I.2. Background

The Indonesian Archipelago can be broadly divided into three zoogeographic regions (**Fig.1-1a**). To the west Sunda, or continental Asia, includes the major Indonesian islands of Sumatra, Borneo, Java and Bali, which were all joined with the Asian mainland during glacial periods of low sea level. To the east Sahul, or Greater

Australia, includes the Indonesian areas of Irian Jaya, Aru and a number of smaller islands, which were connected with Australia during periods of low sea level. In between these two continental regions lies Wallacea, a realm of oceanic islands, including Sulawesi, Flores and Timor, which remained isolated throughout the Quaternary.

Sulawesi is located in the middle of the Indonesian archipelago, which has had a complex tectonic history throughout the Late Cenozoic. The island was formed by the interaction and collision of three major plates; the Indo-Australian, Philippine-Pacific and Asian Plates (Wilson & Moss, 1999; Hall & Wilson, 2000). Sulawesi was separated from the continental island of Borneo by the Makassar Strait, which comprises part of the Wallace Line, the most significant biogeographical boundary in Southeast Asia (Groves, 1985). The tectonic evolution of the region during the Late Cenozoic, combined with eustatic sea level fluctuations, has had major implications for the palaeogeography of Sulawesi and the terrestrial faunal sequence in this region.

Sulawesi, Flores and Timor all had endemic island faunas, which included species of pygmy elephant and giant tortoise (Sondaar, 1984; van den Bergh, 2001). Early hominins also colonised Flores by 0.88 Ma and over time evolved into an endemic hominin species, *Homo floresiensis* (Morwood *et al.* 1998; Brown *et al* 2004; Brumm *et al.* 2006).

Endemic fauna on Sulawesi included *Celebochoerus heeckereni* HOOIJER, which was first described in 1948 based on a fragmentary upper canine from Sompe, South Sulawesi. Since its initial description more teeth and postcranial material became available (Hooijer 1954, 1972), but only fragmentary skull material. During the early 1990s a large number of fossils were collected by an Indonesian-Dutch research group

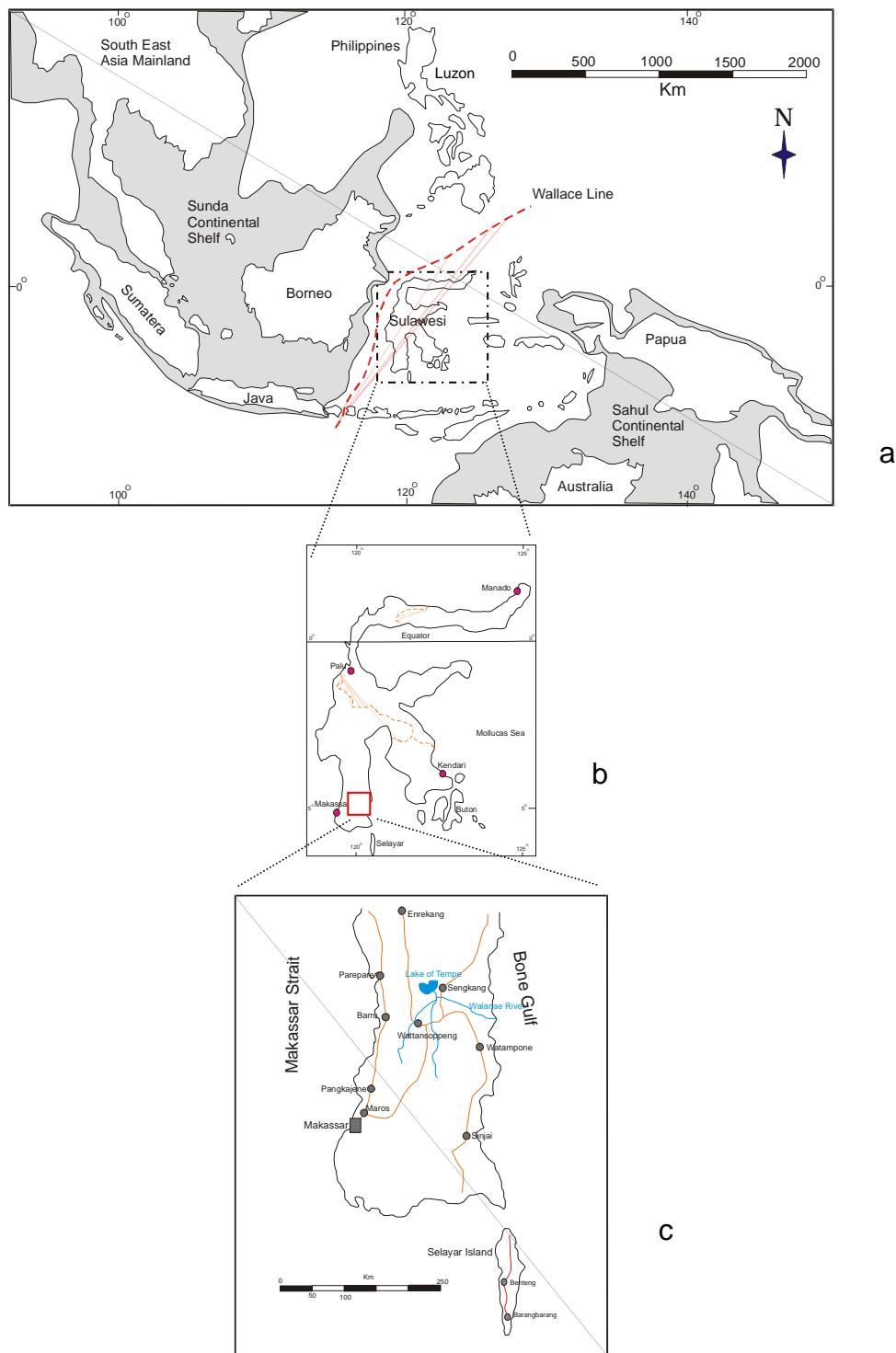


Figure 1-1. (a) Location of the study area showing the Indonesian Archipelago, the Wallace Line, Sunda and Sahul; (b); Sulawesi with the four province capitals; (c) The Sengkang Basin research area in the Soppeng Regency in South Sulawesi.

from excavations and as surface finds at several localities. A preliminary age of the fossil-bearing sequence was also established, suggesting that *Celebochoerus* lived in South Sulawesi between 2.5 and 0.8 Ma. This material has not yet been described in detail. In particular a number of partial skulls collected in the 1990s and during fieldwork in 2008 provides new evidence for the taxonomic position of *Celebochoerus*.

I.3. Significance

There are several fundamental questions concerning *Celebochorus heekerei*, including the species' taxonomy, chronostratigraphy and environmental setting. Like the modern land mammal fauna of Sulawesi, the prehistoric faunas from the island are characterized by a high degree of endemism, reflecting the longstanding isolation of the island. Previous studies have shown that animals represented in the Walanae Formation most resemble those known from the Miocene and Pliocene Siwaliks Beds of India and the Upper Pliocene of Java (Hooijer, 1954; van den Bergh, 1999).

Celebochoerus has a primitive dental morphology. However, its affiliation with other primitive suidae remains poorly known, and is complicated by traits that appear to have evolved independently in isolation on Sulawesi. For instance, its very large upper canines resemble those of the African warthog, *Phacochoerus*, but are likely to be a derived trait developed independently because of similar functional requirements. So far, no closely related suids are known from Java, but scanty dental remains from Luzon in the Philippines may point to the presence of a closely related species there. The study of *Celebochoerus* skull material that remained undescribed so far, may reveal affinities with other fossil and extant suid genera, and shed light on functional adaptations.

We do not know when and how *Celebochoerus* reached Sulawesi, what its direct mainland ancestors were, and when it became extinct. We do know however, that the *Celebochoerus* lineage was present in South Sulawesi over a minimum period of 1.7 million years. Our study may reveal possible adaptive radiations or evolutionary trends that developed during this time span.

Amongst the thousands of fossils collected from the Walanae Formation, none have yet been attributed to *Babyrousa*, an extant endemic pig from Sulawesi, considered to be the most primitive living member of the family Suidae (Groves, 1976, 1981). In Late Pleistocene deposits of Southwest Sulawesi, such as Leang Burung 2 *Celebochoerus* is absent (Glover, 1981). At this site, the sequence spanning the last 35,000 years contains the remains of *Babyrousa*. Recent excavations at this site have extended the maximum age of human occupation and presence of *Babyrousa* to ~100 ka, but still did not yield any *Celebochoerus* remains. In addition, a second suid, *Sus celebensis*, is still extant on Sulawesi, considered to be amongst the most primitive living species of the genus *Sus*.

Comparison of *Celebochoerus* skull material with recent skulls of *Babyrousa* may shed new light on possible taxonomic relationships. Is it possible that *Celebochoerus* was an ancestral species to *Babyrousa*? If not, what alternative explanations can help illuminate the intriguing succession of pigs in South Sulawesi?

It is further expected that the study of *Celebochoerus*, in stratigraphic and sedimentological context, will further provide information on the environmental adaptations and functional morphology of this species. As a case study, evidence for the life, times and extinction of *Celebochoerus* will have implications for the

biogeography and evolutionary history of the other species extinct and extant in the region.

I.4. Methodology

The methods used to collect evidence for this study include:

1. Fieldwork in the Sengkang Basin of South Sulawesi to collect fossil *Celebochoerus* remains; samples for dating; and palaeo-environmental evidence. July to August 2008.
2. Use of published and archival resources.
3. Description and measurement of *Celebochoerus* fossils in the laboratories of the Geology Museum, Bandung. October 2008 to March 2009.
4. Comparative study and measurement of other fossil and recent Suidae remains. October 2008 to March 2009.

I.5. Resources

The fieldwork was financially supported by an Australian Research Council grant to Prof. Mike Morwood, University of Wollongong (UoW) and by the Indonesian Geological Survey Institute (GSI; formerly GRDC) Bandung. The *Celebochoerus* and other suid remains that I described and measured for this thesis are held in the collections of the Indonesian Geological Survey Institute in Bandung, at the Australian National University in Canberra (ANU); and at the Museum Zoologicum Bogoriense (MZB) at Cibinong, West Java.

I.6. Thesis outline and Timetable

Thesis outline

Chapter	Description
Chapter One	Introduction
Chapter Two	Methodology
Chapter Three	Geological framework – Indonesian tectonics; description of Sulawesi stratigraphy and sedimentology.
Chapter Four	Taxonomy of the Suidae, extant and extinct
Chapter Five	Fossils pigs from South Sulawesi, description of <i>Celebochoerus</i> material and comparisons with <i>Babyrousa</i> and other Suidae
Chapter Six	Discussion and Conclusion
References	

CHAPTER TWO METHODOLOGY

This chapter will describe the aims and various methods used in my fieldwork and laboratory analyses. The former includes sampling strategies, recording stratigraphic sections and site descriptions; the latter includes the measurements taken on fossil and recent suid skulls included in this study. The general aim of this work was to reconstruct the chronostratigraphy, paleo-environment, taxonomy and functional anatomy of *Celebochoerus*.

II.1. Field Work

Field work began on July 1st 2008 in the Sengkang Basin, Soppeng Regency, Southwest Sulawesi. The study area lies between 4° 05' S to 4° 26' S and 119° 55' E to 120° 08' E on the eastern margin of the Walanae depression, in between the Western Dividing Range to the west and the Bone Mountains to The East (**Figs. 1-1c; 3-4**).

A geological map of the study was prepared using aerial photographs and 1: 25,000 scale topographic maps from Bakosurtanal (i.e. the Soppeng, Batu-batu, Uloe and Sengkang Quadrangle map sheets). This was followed by the field recording of geological and sedimentological aspects, the drawing of relevant stratigraphic sections and mapping in the field. The regional geology and stratigraphy of the Sengkang Basin are described in Chapter Three.

Fossil localities were located using the reports of previous workers (e.g. van Heekeren, 1958; Barstra, 1977, Sartono, 1979; Aziz, 1990, van den Bergh, 1999), as well as information received from local informants. At some localities with abundant fossils

on the surface, we excavated *in situ* fossil material, completed stratigraphic drawings of the excavations, and took sediment samples for palaeomagnetic, pollen, and micro fossil analyses in the laboratories of the Geological Survey Institute (GSI; formerly GRDC), Bandung. Collected fossils were numbered, labeled in the field and further prepared and catalogued in the Geology Museum, Bandung.

II.2. Studied Material

The material studied included some specimens I collected during fieldwork, but also material housed in the GSI collections. For comparison recent cranial suid material held in the Museum Zoologicum Bogoriense at Cibinong (MZB), Indonesia and in the collection of the Archaeology and Anthropology Department of the Australian National University was used.

Methods for measuring morphological and biometrical parameters of *Celebochoerus* teeth and skulls are largely based on those of Hardjasasmita (1987) and Groves (1981). This study focused on skull and dental elements of *Celebochoerus heekereni*, *Babyrousa babyrussa* and some *Sus* materials (*Sus scrofa*, *S. verrucosus* and *Sus barbatus*). Data of other suid genera was exclusively obtained from the existing literature and various internet resources. No postcranials were studied. Information on the taxonomy, description, and comparative analyses of various recent and extinct suid genera is provided in chapter IV, while new descriptions and measurements on *Celebochoerus* fossil material is provided in Chapter V.

Linear Measurement

Standard Measurements were taken with Mitutoyo calipers (accuracy 0.05 mm), which can measure objects varying between a minimum of 150 mm and a maximum

of 500 mm. The figures showing the measurements taken on skulls (**Figs. 2-1 until 2-5**), are redrawn from Sisson and Grossman (1953) (vide Hardjasasmita, 1987). Morphology and supplementary measurements will be explained in the text where required. Values of estimated measurements are followed by “e”; Minimum values of incomplete measurements are followed by “+”, indicating that the actual value was larger.

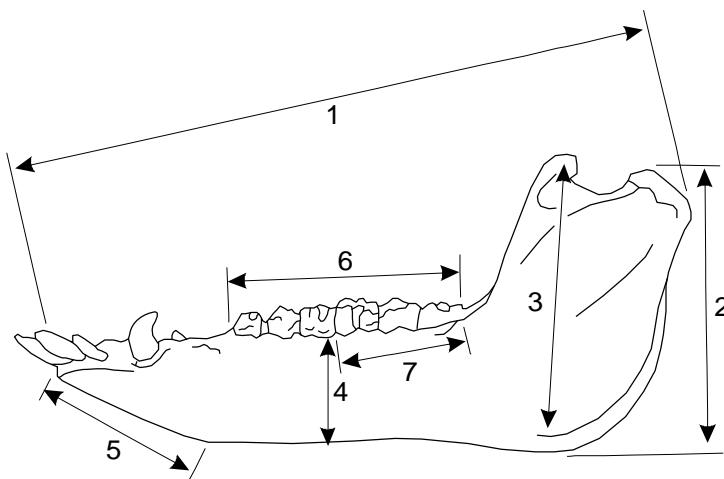


Fig.2-1. Left lower jaw of *Sus*: 1. Length of lower jaw; 2. height of lower jaw; 3. height of coronoid; 4. height of horizontal ramus at the level between P₄ and M₁; 5. length of symphysis; 6. length of P₂ to M₃; 7. Length of M₁ to M₃.

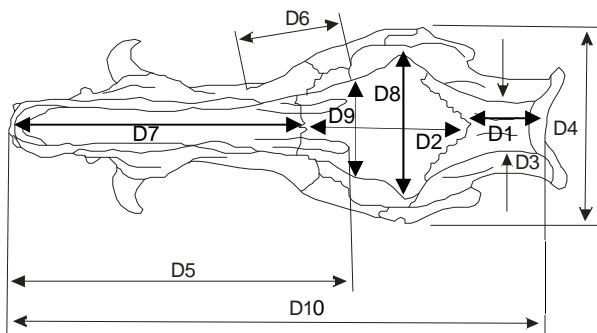


Fig.2-2. Dorsal view *Sus* skull: D1. Length between fronto-parietal suture and occipital crest; D2. Sagittal length frontal D3. Minimum width between the temporal crests; D4. bizygomatic width; D5. length of rostrum: tip of praemaxilla to the point between supraorbital foramina; D6. lacrimal to infralacrimal length; D7. Length of nasal; D8: Transverse distance between the two tips of the postorbital processes; D9. Minimum width between the orbitals; D10. Length of skull from tip of praemaxilla to occipital crest along a sagittal plane.

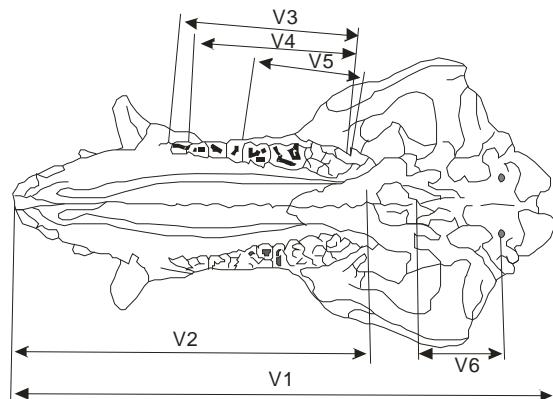


Fig. 2-3. Ventral view of *Sus* skull: V1. condylo – basal length; V2. length of palatine; V3. Length of P^1 to M^3 ; V4. Length of P^2 to M^3 ; V5. Length of M^1 to M^3 ; V6. length of basioccipito-paraphenoid.

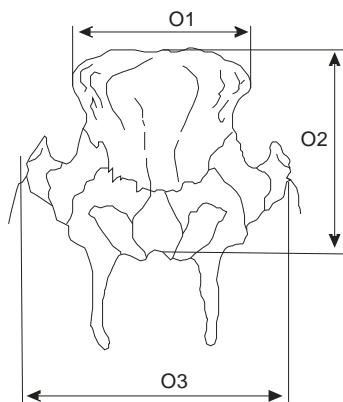


Fig. 2-4. Posterior view of *Sus* skull: O1. width of occipital crest; O2. occipital height; O3. temporal width.

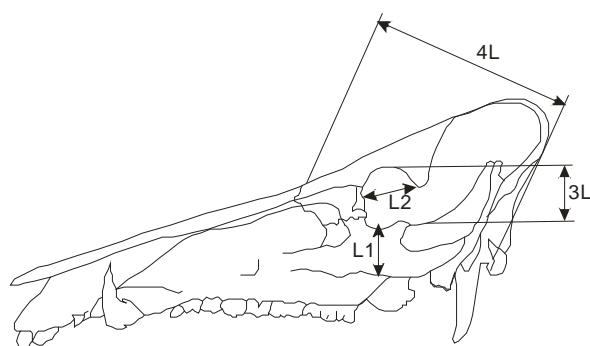


Fig. 2-5. Lateral view of *Sus* skull: L1. Minimum width of jugal; L2. Width of orbital between anterior margin of post orbital process and lachrymal; L3. Height of orbital; L4. distance between fronto nasal suture and ventral margin of the foramen magnum.

Comparison

The morphological nomenclature for describing features of molars and teeth is shown in **Fig. 2-6**. Measurements taken on dental elements are shown in **Fig. 2-7**, they include:

1. Length of each *molar*, *premolar* and *canine*, measured at the base of the crown in *mesio-distal* direction with horizontal position of calliper to the teeth.
2. Width of each *molar*, and *premolar*, measured at the base of the crown in *bucco-lingual* direction with horizontal position of the calliper.
3. Total length of the tooth row, measured in *mesio-distal* direction with horizontal position of the calliper to the teeth.
4. The length of the molar row between the anterior margin of the M1 and the posterior margin of the M3.
5. Height of molars was recorded in unworn specimens only, measured vertically from the base of the crown to highest tip of the cusps.

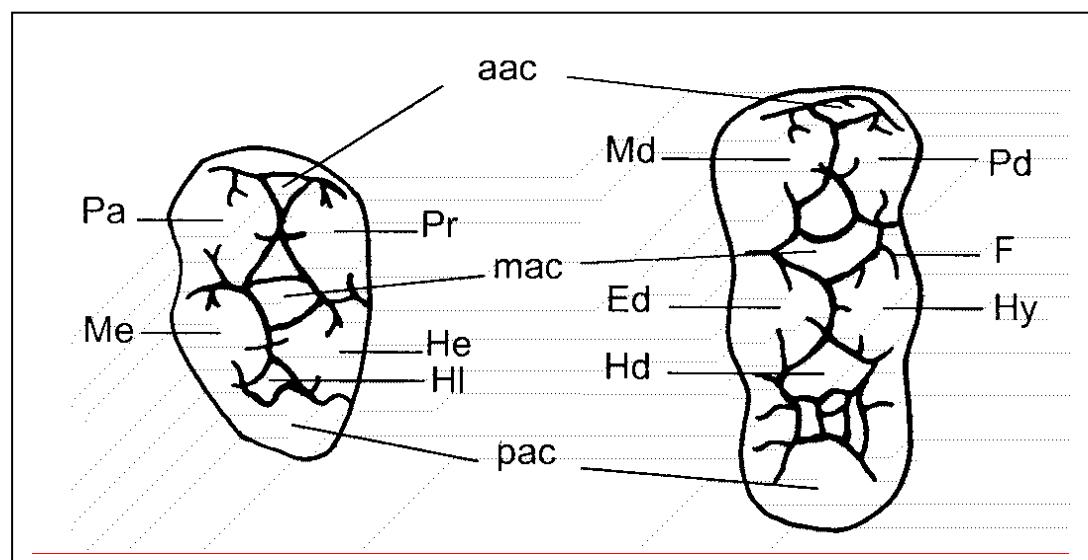


Fig. 2-6. Terminology of the right last upper (left) and lower (right) molars in Suidae (after Liu et al., 2002). Pr = Protocone, Pd = protoconid, He = Hypocone, Hy = Hypoconid, Pa = Paracone, Me = Metacone, Md = Metaconid, Ed = Entoconid, HI = Hypoconule, Hd = Hypoconulid, aac = anterior accessory cusp, mac = median accessory cusp, pac = posterior accessory cusp, F = Furchen.

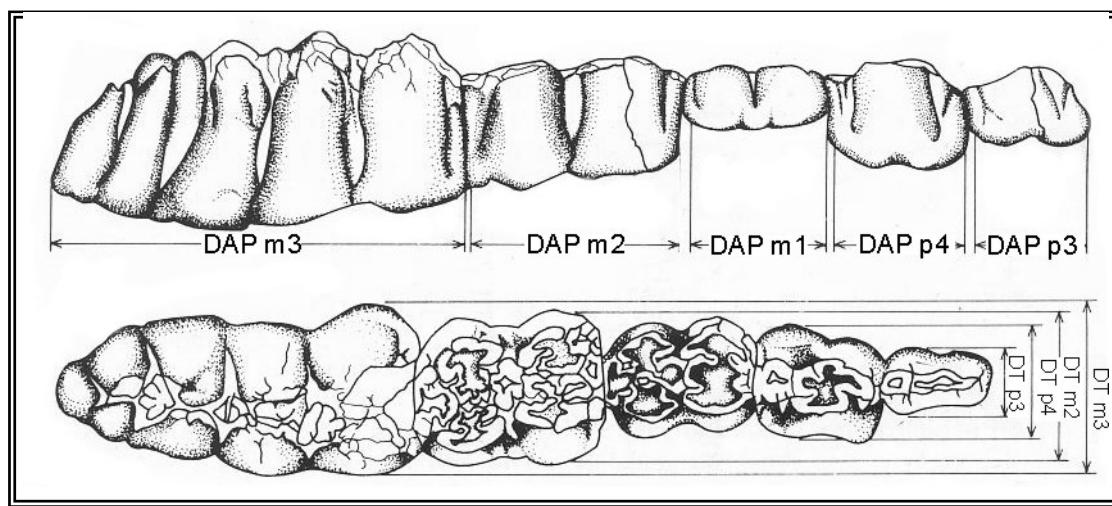


Fig. 2-7. Measurements of suid lower molars and premolars: DAP: length of molar/premolar; DT: width of molar/premolar.

The results of all measurements were corrected by statistical formula including the mean values of each sample (M) together with their standard deviation (sd). In order to compare the relative variability in certain groups, the formula used for the coefficient of variation, which gives the variation (δ)² as a percentage of the average value of the parameter (Table. 2) is as follows:

Table 2. Statistical formula for measurement correction

$$\text{Variance } (\delta)^2 = \frac{\sum (x-\mu)^2}{N}$$

$$\text{Standard deviation (sd)} \delta = \sqrt{\frac{\sum (x-\mu)^2}{N}}$$

$$\text{Coefficient of Variation} = \frac{\text{sd}}{\text{Mean}} \times 100$$

CHAPTER THREE

GEOLOGICAL FRAMEWORK

III.1. Introduction

This chapter will describe the geology, stratigraphy and tectonic setting of the Indonesian region, with particular reference to the divergence of Borneo and Sulawesi through the Cainozoic. Evidence from eastern Borneo, the south-western part of Sulawesi, the Makassar Strait and the Banggai-Sula Platform is particularly relevant.

A range of evidence, including recently published data, will be used to reconstruct the palaeogeographical history of the region and assess the probability, timing and extent of ‘land bridges’ between Sulawesi and the Asian mainland. Such land bridges could have served as migration routes for animals reaching the island, including *Celebochoerus*.

My regional synthesis will be followed by a more focussed description of the stratigraphy and sedimentology in the Sengkang Basin, to establish the age and palaeoenvironmental context of the area’s fossil deposits. This evidence shed light on faunal changes evident in the Sengkang Basin fossil sequence and the associated depositional environments. In fact, the basic aim of this chapter is to detail the life, times and extinction of *Celebochoerus* and associated vertebrate species.

III.2. Tectonic setting

Eastern Indonesia lies on the contact between three converging major plates, i.e. the Eurasian, Indo-Australian, and Pacific Plates. Charlton (2000) proposed that at 30 Ma

the Australian continental margin commenced collision with the subduction zone in the northern region between Sulawesi in the west and Papua in the east (**Fig.1-1**). The subsequent rotational history of Borneo and Sulawesi, and therefore their relative position, in the Palaeogene is still a matter of debate – interpretations offered include “no rotation” (e.g. Lee and lawyer, 1993, 1995), “clockwise rotation” (Rangin et.al 1990), “counter clockwise rotation” (Haile et.al, 1978; Hamilton, 1979; Hall, 1996 and Charlton, 2000), and “mixed rotations” (Briais et.al, 1993).

During Early Eocene, a land connection existed between southwest Sulawesi, southern Borneo and mainland Southeast Asia. However, later during the Middle Eocene extension in the Makassar Strait Region occurred, which lead to the formation of a deep water basin. Then, in the early Oligocene to Late Miocene, the Australian micro-continental fragments, which now constitute east Sulawesi, began to collide and merge with west Sulawesi, which was largely derived from continental Asia (Hall, 1996; Wilson and Moss, 1999).

At the same time, spreading behind a north dipping subduction zone, which accommodated the northward movement of the Indian Oceanic Plate, formed the Celebes and Philippine Sea marine Basins. This spreading finished in the Late Eocene and by the end of the Late Oligocene both basins were separated by strike slip and later by convergent plate boundaries. In contrast, the West Philippine Sea Basin subsequently underwent clockwise rotation towards its present position (Nichols and Hall, 1999). The Philippine Archipelago has, therefore, been separated by deep-sea barriers from North Asian Mainland for the last 60 million years – as a result northern routes for colonisation of Sulawesi were always difficult (Audley and Charles, 1981).

III.2.1. Makassar Strait

The geological history of the Makassar Strait is fundamental to understanding how and when animals cross from the Asian mainland to Sulawesi. It also has implications for the source of the tertiary basin infill of the Kutai Basin to the west and Sengkang Basin in the east.

The Makassar Strait can be divided into three physiographic regions – 1) the shallow Paternoster Platform, 2) the North Makassar Basin, 3) South Makassar Basin. The latter two basins are connected by a central deep water trough with depths around 1500 to 2500 m, and a very narrow and steep slope along the western Sulawesi margin (**Fig. 3-1**).

The tectonic evolution of the region has been debated since Alfred Russell Wallace first delineated his Australian-Asian faunal boundary (i.e. the Wallace Line) along its axial. The mechanisms and age of the tectonic processes involved are also subject to considerable scientific debate. However, most researchers support extensional origins, with estimated ages for rifting varying from Middle Eocene (Situmorang, 1982; Hutchinson, 1989; Rangin et al 1990; Hall, 1996; and Moss et al, 1997), to Miocene (Bendang, 1993; Groves, 1981), Pliocene (Katili, 1971) to Quaternary (Van Bemmelen, 1949).

Hamilton (1979) assumed that the South and North Makassar Basin were formed by extensions; resulting from the Adang Transform fault. Malecek et al (1993) proposed that a fragment of Late Cretaceous oceanic crust was trapped between the relict subduction zones of northwest Borneo and western Sulawesi. To determine the type of crust beneath the basins, the distribution patterns of basement terranes, plate motion vectors and structural deformation have been analysed by Cloke et al (1999).

Bergman et al, (1996) applied an advanced further method of flexural modelling to interpret the tectonic history of the Makassar Strait region; they then argued that the North Makassar Basin could be interpreted as an actively forming foreland basin located immediately in front of the Majene Fold Belt. This setting can be explained by

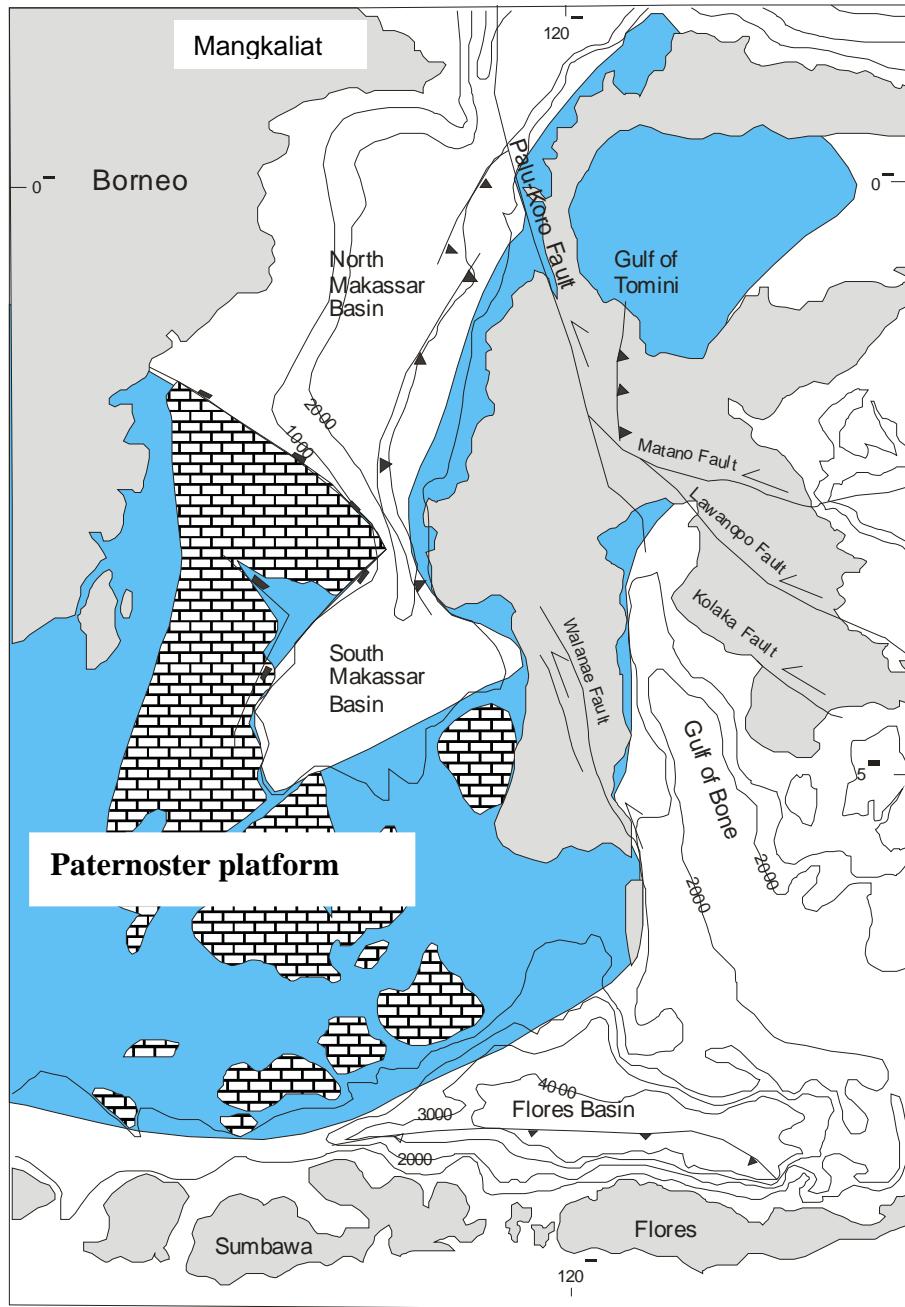


Fig.3-1. The tectonic setting of Borneo, Makassar Strait and Sulawesi Island, modified from Letouzey et al, 1990; Kavalieries et al 1992; Bergman et al (1996); Hall (1996); Parkinson 1996 and Charlton, 2000). Blue area represents terranes of presumed Sunda origin.

the combined effect of Late Neogene thrust loading in western Sulawesi with sediment loading in eastern Borneo associated with the development of the Mahakam delta, resulting in crustal subsidence along much of the Makassar Strait (see **Fig. 3-1**).

III.2.2. Borneo

Subduction along the Sundaland margin can be traced back into Pre-Tertiary times, as evidenced by metamorphic rocks exposed in the Meratus Mountains (southeast Borneo) – and associated accretionary complex. The turbidite lithologies in this area indicate a remnant oceanic basin depositional setting (Moss and Wilson, 1998). In addition, Cretaceous shelf sandstone, limestone, Triassic granite, and older metamorphic rocks are exposed in the central Borneo Range (Pieters and Supriatna, 1990) that may represent back arc oceanic material, as well as associated accreted sedimentary and volcanic rocks that may have been thrust onto the eastern margin of Sunda in the Early Cretaceous (Sikumbang, 1986, 1990).

During the Late cretaceous to Eocene period, the deposition of turbidite sequences (Rajang and Embaluh groups) is evident in outcrops of the Eastern and Central Borneo Ranges, e.g. at Longbia and Malinau. These outcrops are characterized by steep tilting, intensive deformation, and metamorphism (slate, meta-sandstone). At the same time, western Sulawesi was accreted onto eastern and southern Borneo and land connected the Schwaner Mountains (north-western Borneo) and the Mangkaliat Peninsula. Borneo at that time was a peninsula on the eastern and southern margins of Sunda, which constituted the stable margin of the Eurasia Plate during the Tertiary, when it was covered by sedimentary rocks deposited in fluvial, marginal-marine, lacustrine or marine environments (**Fig. 3-2**).

Furthermore, the rifting of the Makassar Strait and the formation of surrounding deep water basins in the Tertiary (i.e. North and South Makassar Basin (NMB & SMB) resulted in the progressive separation of land between Borneo and western Sulawesi.

III.2.3. Celebes Sea

In the Celebes Sea, stratigraphic and regional tectonic provides the basis for the reconstruction of possible faunal migration routes from Borneo and the southern Philippines to Sulawesi. However, the complex tectonic setting during the Tertiary makes it difficult to work out the origin and history of individual terranes like the Sulu, Sangihe and Talaud Islands.

Nichols and Hall (1999) argued that the Celebes Sea and West Philippine Basins were formed by spreading behind a north dipping subduction zone compliant with the northward movement of the Indian Ocean Plate in the Middle Eocene. During the Late Eocene to the End of the Oligocene, the Celebes and West Philippine Basins were separated by strike-slip fault zones and later by convergent plate boundaries. Throughout Early to Middle Miocene sedimentation in both basins was dominated by pelagic deposition with very slow deposition and lacking substantial input from terrigenous siliciclastic or volcanic sources.

Based on ODP core 124 and the observed timing of cessation of volcanism, Silver et.al (1991) proposed that the Sulu Sea subducted southward along the Sulu Arc from 15 to 10 Ma. The northwest Sulu Basin trapped the clastic sediments derived from the Cagayan-Reed Bank collision (**Fig. 3-3**).

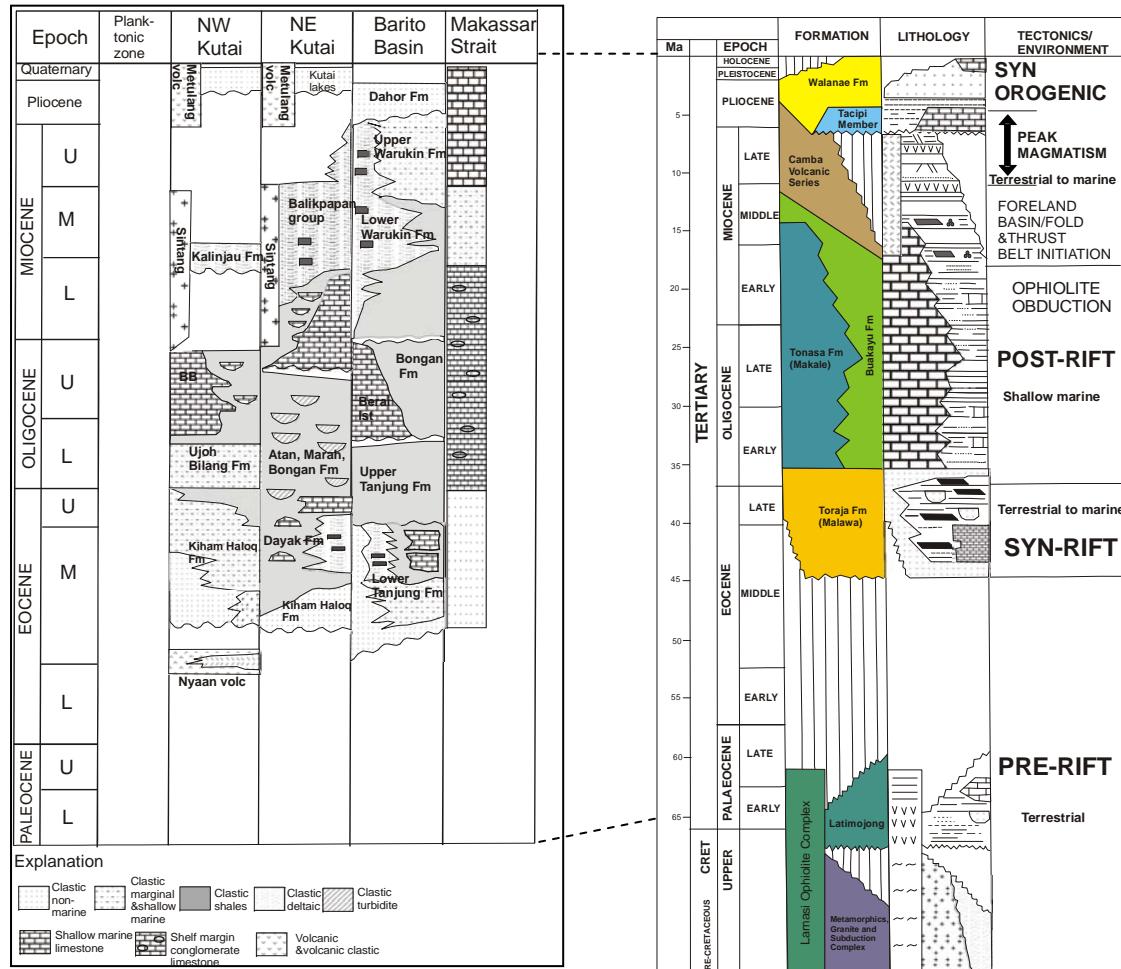


Fig.3-2.Stratigraphic column for eastern Borneo, southern Borneo and Makassar Strait and southwest Sulawesi redrawn from Wilson and Moss, 1999 and Guntoro, 1999.

In other parts, major renewal of volcanic activity in North Sulawesi is interpreted as the initial southward subduction of the Celebes Basin and collision of the Sulu Arc

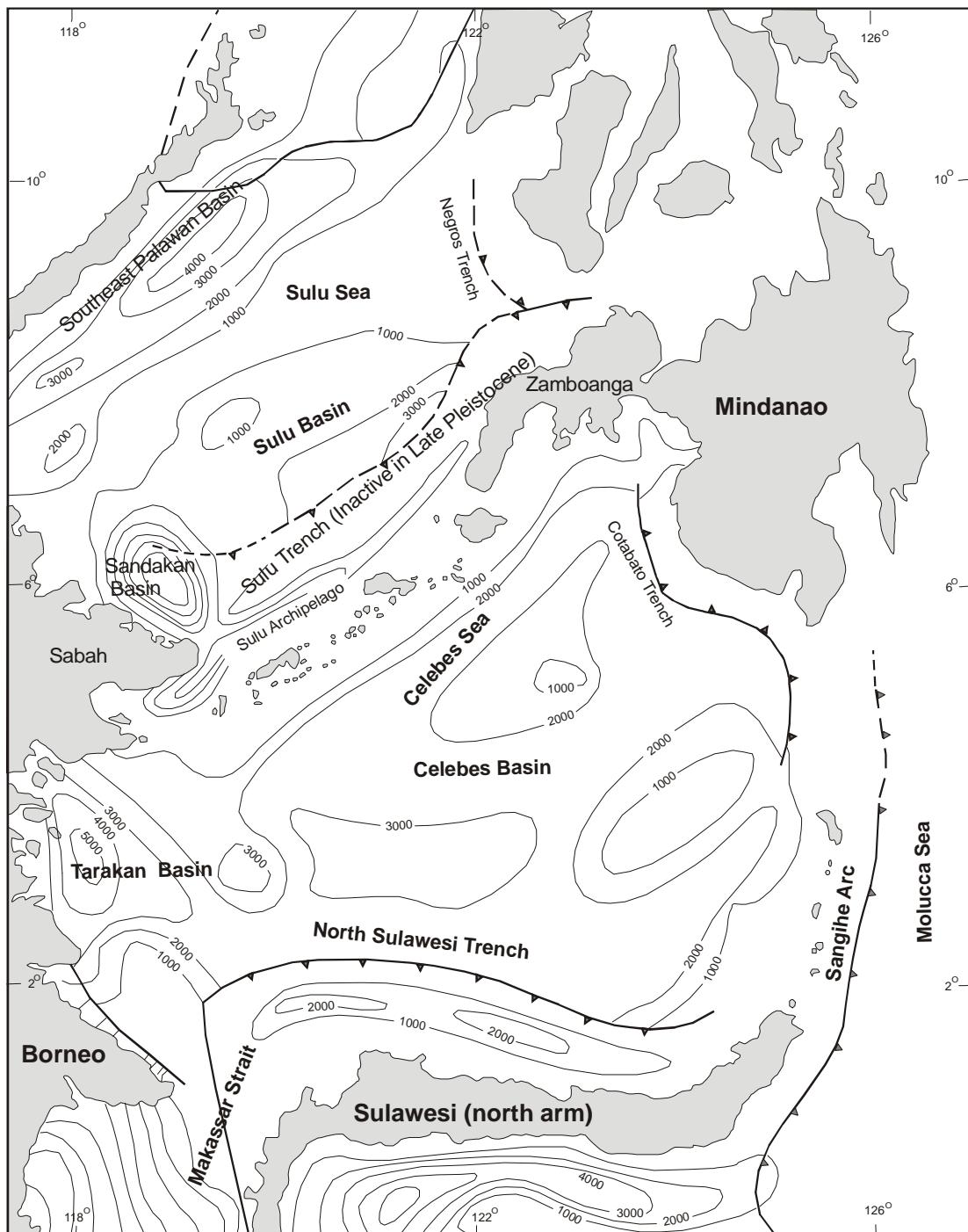


Fig.3-3. Map of the Celebes Basins and surrounding areas showing the present bathymetry (1000-5000 m depth contour) and the main tectonic setting features discussed in the text (redrawn from van der Kaars, 1991; Rangin and Silver, 1991).

with Eurasia at Sabah and Palawan, which induced massive quartz turbidite deposition in both basins. The source of these turbidite clastics is detritus reworked as second cycle material from the eastern margin of Borneo that is interpreted as uplifted terrains in eastern Borneo before late Miocene times.

III.2.4. Sulawesi

Sulawesi formed along the Oligocene – Miocene collision between the Eurasian Plate and micro-continental fragments derived from the Indian-Australian Plate. It can be divided into four arms, each characterized by different tectonic provinces (Hamilton, 1979; Rangin et al 1990; Parkinson, 1991; Bergman et al, 1996; Simandjuntak and Barber, 1996; Hall, 1996). The northern arm consists of volcanic rocks related to Late Palaeogene to Neogene subduction of the west dipping Moluccas Sea Plate (**Fig. 3-3**). Largely contemporaneous with these rocks are limestone and clastic sediments. In the southwest arms, Tertiary deposit such as the Tonasa Limestone, Miocene to Younger volcanics and clastic sediments cover a Mesozoic basement representing the south-eastern margin of Sunda (**Fig. 3-2**).

The northern and southern arms are here referred to as “western Sulawesi” for simplicity. The east and southeast arms have an oceanic origin and are composed of Mesozoic and younger allochthonous metamorphic and ophiolitic rocks, which were obducted onto western Sulawesi during the Oligocene to Early Miocene. In addition, there are several small continental fragments which have collided with eastern Sulawesi, including Banggai-Sula, Tukang Besi and Buton.

Geologically, southwest Sulawesi was formed during the Early Cretaceous as a basement complex, and apparently includes old continental crust of Australian origin.

This is supported by the presence recycled ancient zircons from Miocene igneous rocks, which on the basis of their chemical composition, originated from northern Australia, not from Southeast Sundaland. Possibly, these became accreted onto Sunda during the Oligocene to Miocene collision event (Bergman et.al, 1996; Priadi et.al 1993).

During the Middle to Late Eocene, the basement west of the Walanae depression was covered unconformably by volcanic and marginal marine coal-bearing deposits of the Malawa or Toraja Formation (Sukamto, 1982). Later, during the Oligocene, the Tonasa Formation (**Figs. 3-2, 3-4**) indicates the development of extensive areas of shallow water carbonate platforms in southern Sulawesi, whilst deep water marls were deposited in adjacent areas (Supriatna et al, 1993; Wilson, 1995). Contemporaneous carbonate platform are also found in the East Java Basin and southern Borneo Basin, where tectonic activity is recorded by the lateral deposition of reworked carbonate facies in the down faulted blocks. This deposition continued until the Middle Miocene (Wilson and Bosence, 1996; Kusuma and Darin, 1989).

The igneous rocks of Camba-Enrekang-Mamasa volcanic complex and derivative volcaniclastic deposited cover more than 75 % of the surface of western Sulawesi in Middle to Late Miocene times. This volcanism was related to a north-south trending volcanic arc system. Analysis of trace elements indicates that the Miocene igneous rocks are subduction- related, associated with compressional boundaries, in which oceanic crust is subducted beneath continental crust.

Locally, small carbonate reefs of the Tacipi Member formed in the East Sengkang Basin, where this shallow marine facies interfingers, or overlies marine clays representing the base of the Walanae Formation (Late Miocene). These clays

accumulated in the down faulted Walanae depression and north of Bone Mountain (Grainge and Davis, 1985; van den Bergh, 1999). During the Pliocene, the structural evolution of South Sulawesi was probably characterized by compressive deformation, started by Miocene collision with East Sulawesi, which produced post collisional uplift and nappe obduction by low and high angle normal faulting (Harris, 1989 and Bergman et al 1996).

The Lamasi Ophiolite Complex in western Sulawesi and the analogous ophiolite in the eastern arm are separated by the deep intervening Bone Bay, suggesting that orogenic collapse may have occurred here. Thus, local compressive forces were still active until Late Miocene to Recent times.

A major NNW – SSE trending fault system, the Walanae Fault Zone, separated the eastern and western parts of South Sulawesi and influenced deposition during the Late Miocene to Quaternary (**Fig. 3-4**). Grainge and Davies (1985) suggested that this fault consists of two major components - a western part, designated as West Walanae Fault (WWF) and an eastern part as East Walanae Fault (EWF). Furthermore, they divided the Late Cainozoic basin on both sides of the EWF into the West and East Sengkang Basins (WSB and ESB). The WSB corresponds with the Walanae and Lake Tempe depression.

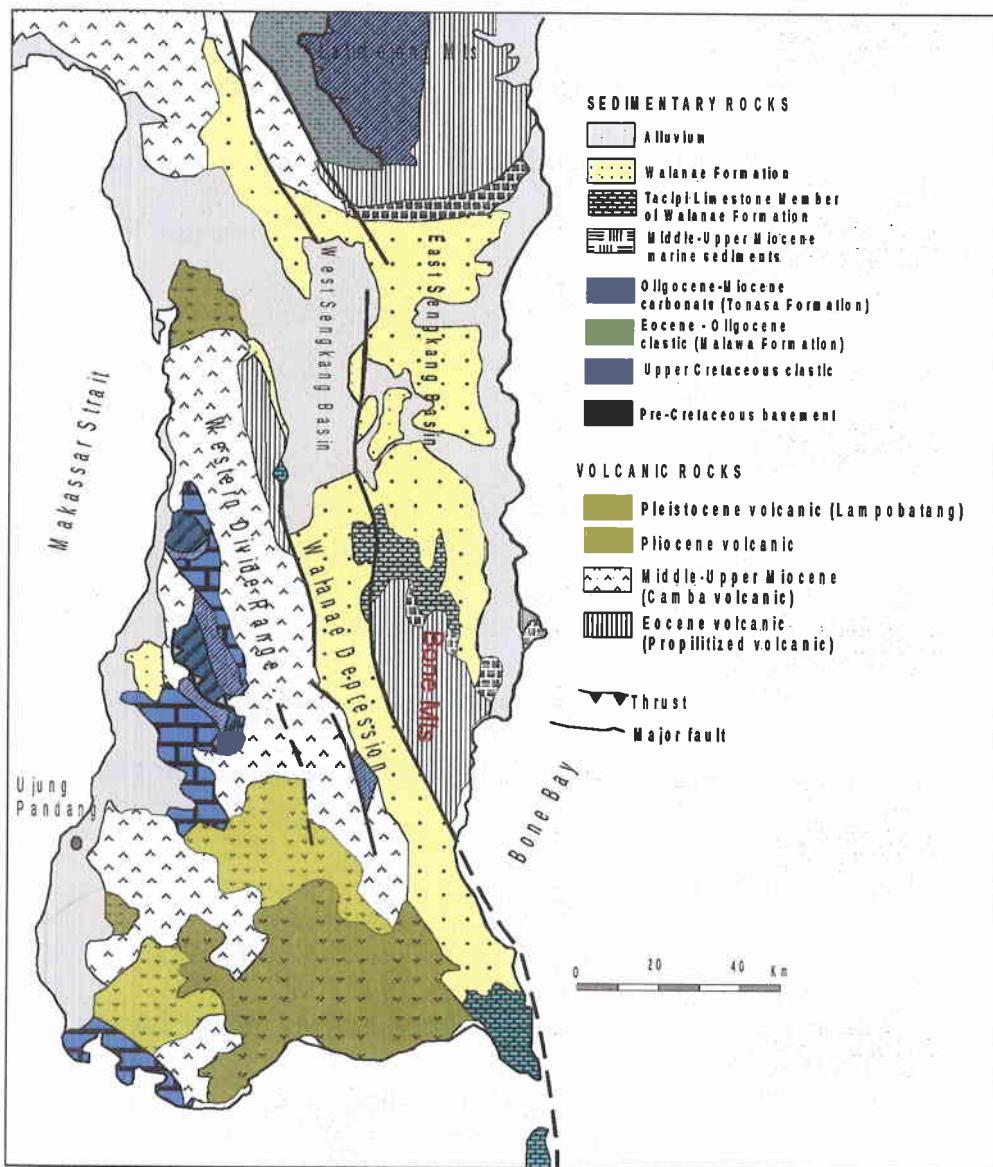


Fig.3-4. Geological map of South Sulawesi (adopted from Sukamto, 1975, van Leeuwen, 1981, Bergman et al 1996; van den Bergh, 1999).

III.3. Exposed land Areas: When and Where?

This section is concerned with Indonesian palaeogeography, especially in the Sulawesi region during the Miocene, Pliocene and Pleistocene – as based on geology, sedimentology, and pollen evidence. The aim is to assess a palaeogeographic disposition of South Sulawesi as a result of tectonic plate movements and/or changes in global sea level. If land bridges ever existed, they would have facilitated faunal colonisation of Sulawesi.

Early Tertiary

The palaeogeographic evolution of East Sunda can be used to explain mammal migrations to Sulawesi, either through northern routes from Taiwan and the Philippines via the Sangihe Arc or Sulu Archipelago to north Sulawesi, or through a western route from Sunda across the water barrier of the Makassar Strait to western Sulawesi.

Based on the regional geological data from East Borneo and Makassar Strait, western Sulawesi formed part of the eastern Sunda margin during the Cretaceous to Early Eocene, when there was a land connection between north-western Borneo, the Schwanner Mountains, the Mangkaliat Peninsula and West Sulawesi. This is indicated by similar characteristics of ophiolite in the Meratus Complex west of Makassar Strait and Bantimala east of it. The deposition of the Malawa Formation (coal bearing deposits in South Sulawesi) is interpreted as generated during syn-rift processes of spreading between Borneo and western Sulawesi, and South Sulawesi formed an

isolated island during the Late Eocene (**Fig. 3-2**). The deposition of this facies continued until the Early Oligocene. Thus, Borneo and Sulawesi were separated by the rifting of Makassar Strait that started during the Middle Eocene.

In post rifting times, from Early Oligocene to Early Miocene, a shallow marine environment was created in large parts of South Sulawesi, as shown by the Makale and Tonasa limestone formations. The Oligocene clastics in the northern part of South Sulawesi near the Latimojong Mountains, indicate the existence of emerged areas in that region. Bergman et al (1996) assumed that regional east-west compression continued until Pliocene to Recent times, resulting in the development of a Late Neogene fold and thrust belt with slope-related imbrications. This promoted regional uplift rates of $200\text{-}700 \text{ m Ma}^{-1}$ during the last 2-18 Ma, further extending the emerged land area.

Miocene to Early Pliocene

During the Lower Miocene, the Palawan microplate was broken up rapidly southward as the South China Sea opened, to collide with Borneo (Audley-Charles, 1981). The wide water barrier already in place between China and the major Filipino islands would have made faunal dispersals to the islands difficult.

The collision between Sundaland and fragments of the Australian continental margin continued until the Middle Miocene, resulting in the formation of the Banda Arc. Around the same time in Papua New Guinea, the mountains were rapidly uplifted and other islands in eastern Indonesia were raised above sea level (Hall, 1996, Moss and Wilson, 1998).

Evidence of land in western Sulawesi is shown by mountain ranges corresponding with the Camba volcanics during the Middle to Late Miocene (**Fig. 3-5**; Van den Bergh 1999). The Camba volcanics accumulated in the western part of the Walanae Depression in the Early to Late Miocene; a time when the eastern part was predominantly shallow marine, with little land exposed.

Additionally, the regressive sequential development of the Walanae Formation indicates a further gradual emergence of terrestrial environments, at a time when the Makassar Strait was already established as a deep-sea barrier.

A major change in the sedimentation history of the region occurred in the Early to Middle Miocene, when a deltaic environments developed along East Borneo. These deltas prograded eastward during the Miocene until stopped by tectonic uplift in the Late Miocene at approximately 6.6 Ma (**Fig. 3-5**). By the end of the Early Miocene, the Mahakam Formation delta front had advanced approximately 200 km westward from the present day coastline, which brought east Borneo closer to north Central Sulawesi (Moss *et. al*, 1999 in Meijaard, 2003).

In the south and west, the islands of Java and Sumatera slowly emerged from the sea during the Miocene, initially as a chain of small volcanic islands, which were inundated during high Middle Miocene sea levels.

Early Pliocene to Early Pleistocene

In the Early to Middle Pliocene (ca. 4.5-3.5 Ma), there is evidence of much higher sea levels, ~100 m above present-day levels, and Borneo became separated from the Asian mainland (Haq *et al*, 1987; Mc Neill *et al*, 1998). In East Borneo, the Mahakam

River carried a large volume of sediment, which it mainly deposited in a delta, which prograded west throughout the Pliocene, as it does today (**Fig. 3-6**).

Celebochoerus had already crossed to Sulawesi by the Late Pliocene, as evident by fossil remains in the Beru Member of the Walanae Formation, which are estimated to be 2.5 Ma in age (van den Bergh, 1999).

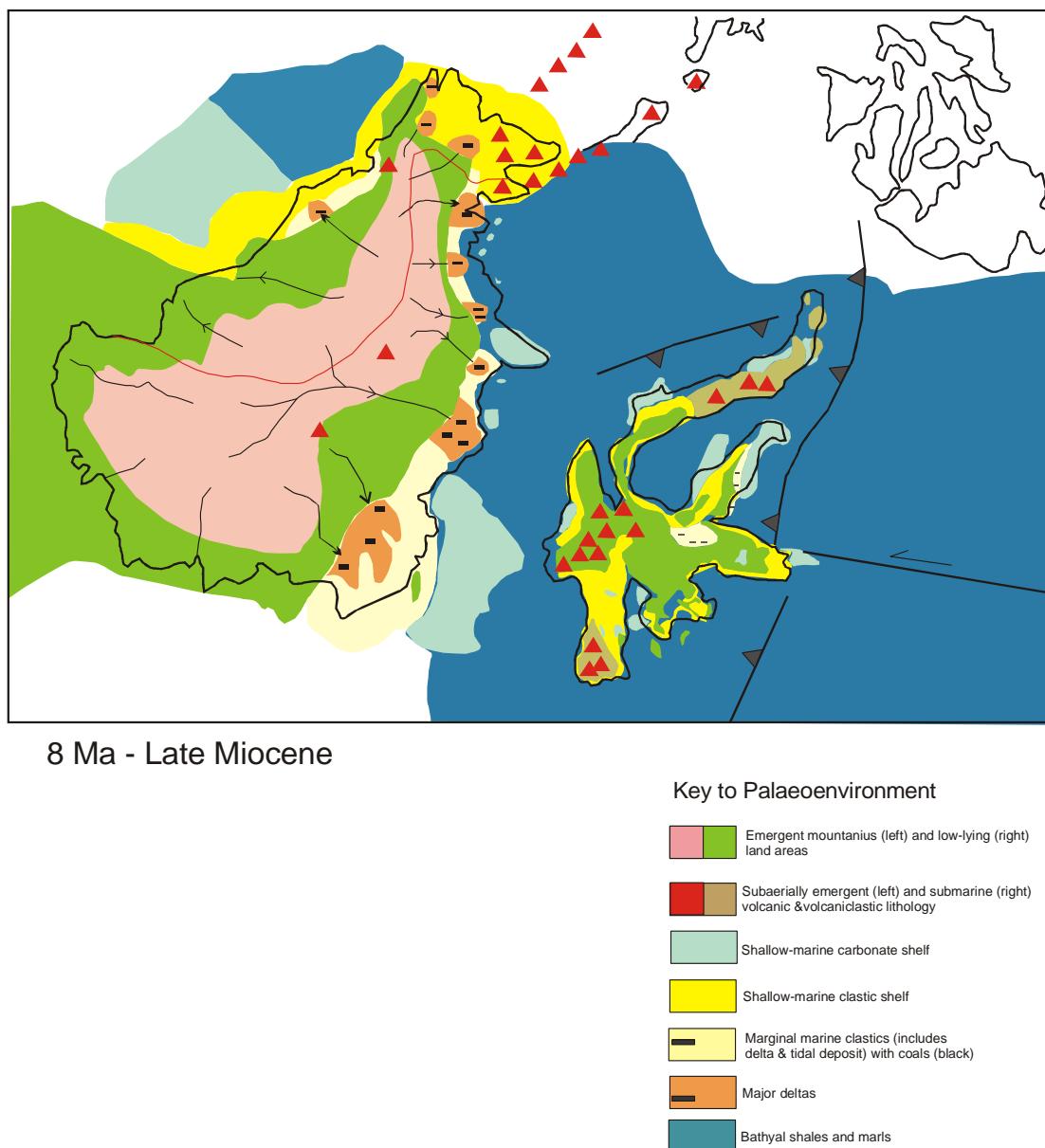


Fig. 3-5 Palaeogeography of Sulawesi in the Late Miocene (redrawn from Moss and Wilson, 1998 and Hall, 1996)

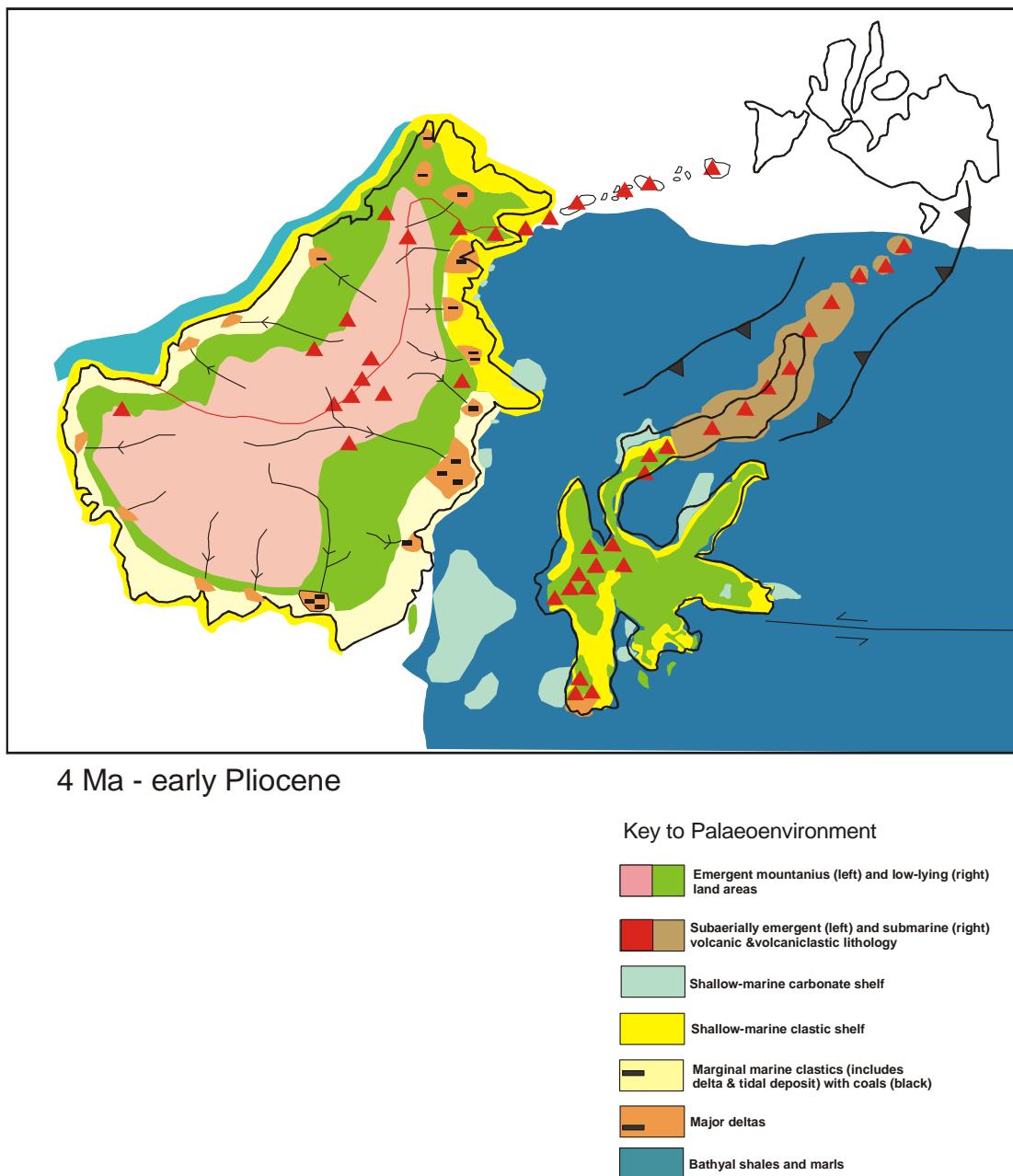


Fig. 3-6. Palaeogeography of Sulawesi in the Early Pliocene (redrawn from Moss and Wilson, 1998 and Hall, 1996)

Early Pleistocene to Recent

The Early Pleistocene to Middle Pleistocene is characterised by fluctuations in climate and in sea level, which fell by up to 100 metres below present sea level. It is also the

time where Java and Sumatera both started to take on their present shape, and when both were connected to the Asian mainland (Meijaard, 2003).

III.4. Stratigraphy and sedimentology of the Sengkang Basin

The Sengkang Basin (or Walanae Depression) is formed by a major of NNW – SSE trending fault system in the Walanae Fault Zone, which was generated by Late Neogene foreland basins or syn-orogenetic deposition. The Late Neogene basin is filled by clastic sediment containing some fossils and where dated is no older than Late Miocene.

Sarasin and Sarasin (1901) named the deposits that filled the Late Neogene sedimentary basins in South, West and Southeast Sulawesi, “Celebes Molasse” (van Bemmelen, 1949). Later, Hoen and Ziegler (1917) used the term ‘Walanae Formation’ for syn-orogenetic molasse deposits in South Sulawesi. The term is used here for the Upper Miocene to Holocene clastic sequence which developed in the Walanae Depression and northern extension in Sengkang Basin. On the basis of seismic profiles, the Walanae Formation unconformably overlies the Late Miocene Camba volcanics (Grainge and Davies, 1985).

Seismic profiles also show that in the centre of West Sengkang Basin, the Walanae Formation comprises a continuous sequence up to the modern floodplain and lake deposits around Lake Tempe (Grainge and Davies, 1985). In addition, reef talus of the Tacipi Limestone interfingers with the lower mudstones of the Walanae Formations (Sukamto, 1982).

III.4.1. Field Data Significance

The Walanae formation is formally divided into Tacipi Limestone Member, Burecing Marine Mud Member, Samaoling Sandy Marine Member and Beru Fluvial Clastic Member by van den Bergh (1999).

In the Soppeng area, the West Sengkang Basin is dominated by calcareous grey clays in the lower part of the Walanae Formation, known as **Burecing Member**, after Burecing Village along the Cabenge – Pampanua road (van den Bergh, 1999). Exposures can also be found along the Lakibong and Walanae Rivers and in Parenring Creek.

These clays are approximately 900 metres thick and contain foraminifera, nanoplankton and marine molluscs, indicative for an open marine, outer sublitoral to upper bathyal deposition environment (see **Appendix 4**). The Burecing Member interfingers with the shallower marine Tacipi Coral Limestone Member locally.

The Samaoling Member is the middle part of Walanae Formation, characterized by an alternation of shallow marine silty mudstones and fine to medium grained well-sorted sandstone. The type locality for the sandy interval between the lower marine and fluvio-deltaic strata is near Samaoling Village. This member is approximately 850 metres thick (**Fig.3-7**).

Massive well-sorted sandstones; with scoured structures, dominate the lower part of the sequence. In the same sequence, intercalation between thin-bedded fine grained sandstones and siltstones is clearly exposed with waves ripple structures and cross laminations. The middle part of the sequence is characterized by parallel laminations of siltstone and claystone but unfortunately, this interval of the Samaoling Member is

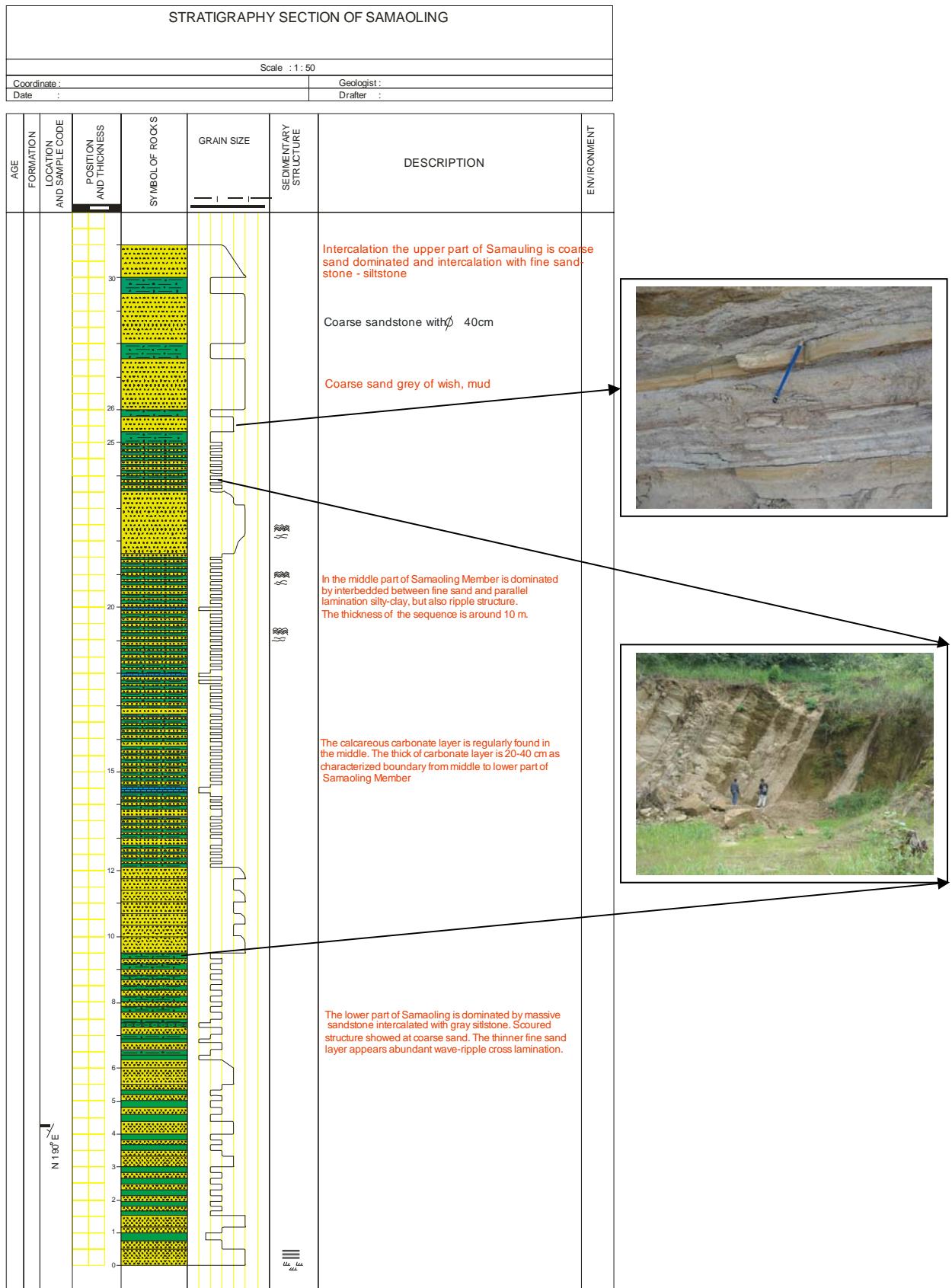


Fig.3-7. Detailed stratigraphic section and photograph of Samaoling member along Cabenge to Pampanua road in the S: $04^{\circ}19'53.4''$ and E: $120^{\circ}01'49.5''$ position. The bedding of this sequence is between 50° and 75° to the northwest.

poorly exposed. A concretionary, calcareous layer, which contains mollusc fossils, lies at the boundary between the lower to middle part of this member. Thick, massive sandstone with alternating silty and clayey layers dominate the upper part.

The deposition of the upper, shallow marine sandstones probably occurred on a shallow marine shelf, in a lagoonal, tidal setting, but open to wave-action and storm currents.

The Beru Member, which unconformably overlies the Samaoling Member, comprises the upper part of the Walanae Formation, and is very rich in vertebrate fossils. Sartono (1979) argued that this member, dominated by sandstones, was formed of Late Pleistocene fluvial deposits that were subsequently shaped into terraces (van Heekeren, 1958; Barstra, 1977 and Sartono, 1979b). On the other hand, van den Bergh maintains that the Beru Member comprises the upper part of the Walanae Formation, as developed along the west flank of the Sengkang anticline and adjacent areas.

The Beru Members is well exposed at Lepangeng Village (S: 04°23'19.2" and E: 120°02'19.4") where, it is characterized by medium to coarse sandstones with pebbles, and a massive and scoured sedimentary structure. It is around 50 m thick and was deformed by tectonic activity, as indicated by tilting of the sandstones with bedding between 54° and 60° to the southwest. About 30 metres to the west, a tide bundle sequence of mud drapes structure is exposed on fine sandstone. The stratigraphic section on the western flank of the Sengkang anticline shows an intercalation between fluvial layers with lagoonal and estuarine deposits, indicating that the area was a transition zone between lagoonal/estuarine and fluvio-lacustrine environments.

The lower Beru member is well exposed near Paroto village, where it consists of fine grained sandstones with mud drape structures (**Fig. 3-8**). These are unconformable overlain by old terraces, which can be divided into unconsolidated examples, dominated by small fragments, and cemented terraces in the upper part characterized by big rock fragments, as well as stone artefacts. The middle sequence of the Beru Member appears to have eroded, and to have been changed from tidal to point bar or bench setting by continued uplift of the basin.

Mega-ripple cross bedding at the transition between the Beru and Samaoling Members shows fluctuations in paleo-current direction but with an E-W trend; these probably reflect ebb tide and flood currents.

A NW-SE seismic profile in the north part of Sengkang Basin shows large-scale, westward-dipping strata, interpreted as Delta foresets (Grange and Davies, 1985). This deltaic sequence reaches the surface in the Sengkang Anticline and can be correlated with Samaoling and Beru member of the Walanae Formations. During the deposition of these members, the north part of the Sengkang Basin gradually changed from a tidal and deltaic to fluvial environment.

In the Bulu Cepo areas, the lower part of the Beru Member is dominated by massive compacted conglomerate, interbedded with carbonate silty-clay-fine sand and with underlying mud drapes structure; while the upper part is cross-bed, fine to medium sandstone. The Beru Member conformably overlays the Samaoling sequence and the boundary is bundle sequence of fine sandstone or mud drapes structure. The dipping of upper part Beru member is slightly, around 6° - 10° . The Beru member is the main source of vertebrate fossils in this region. In fact, during my fieldwork, a *Celebochoerus* canine was found *in situ* in the upper part of this sequence.

Mud drapes structure

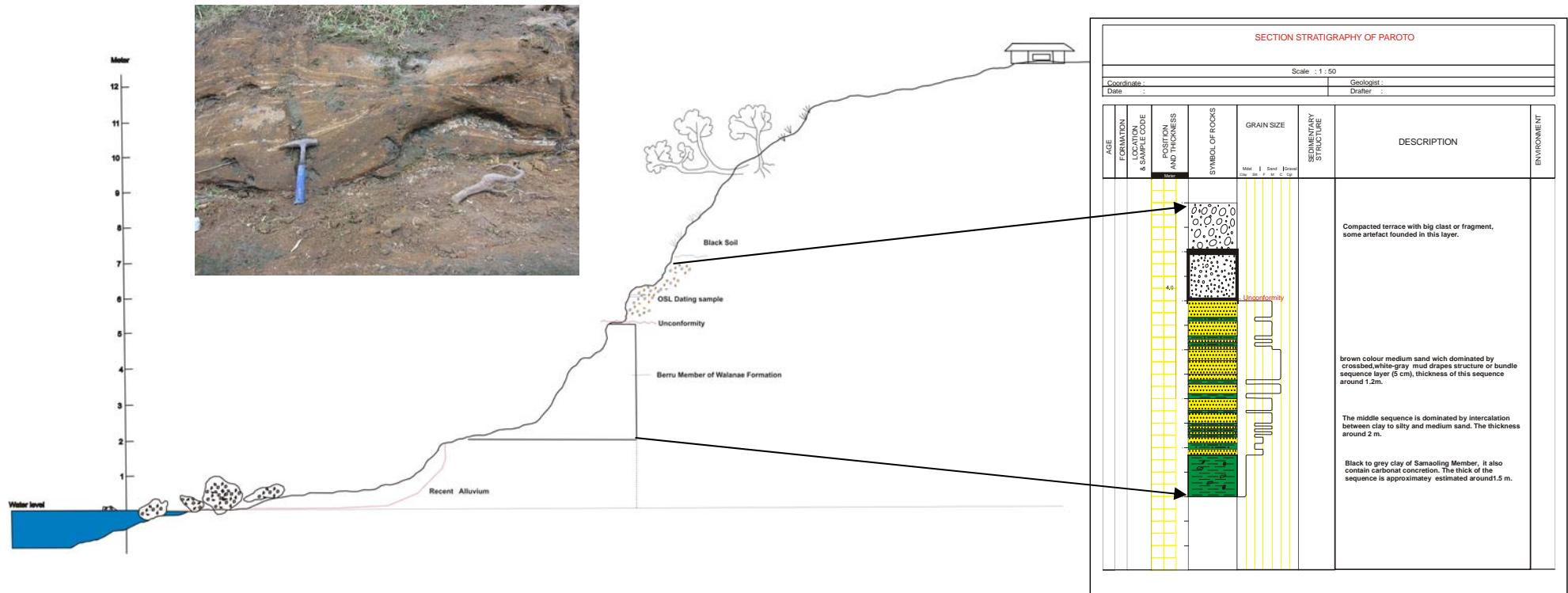


Fig.3-8. Detail stratigraphic section and plan of Beru Member is exposed at Paroto village. The mud drapes structures also founded in the middle part of this sequence.

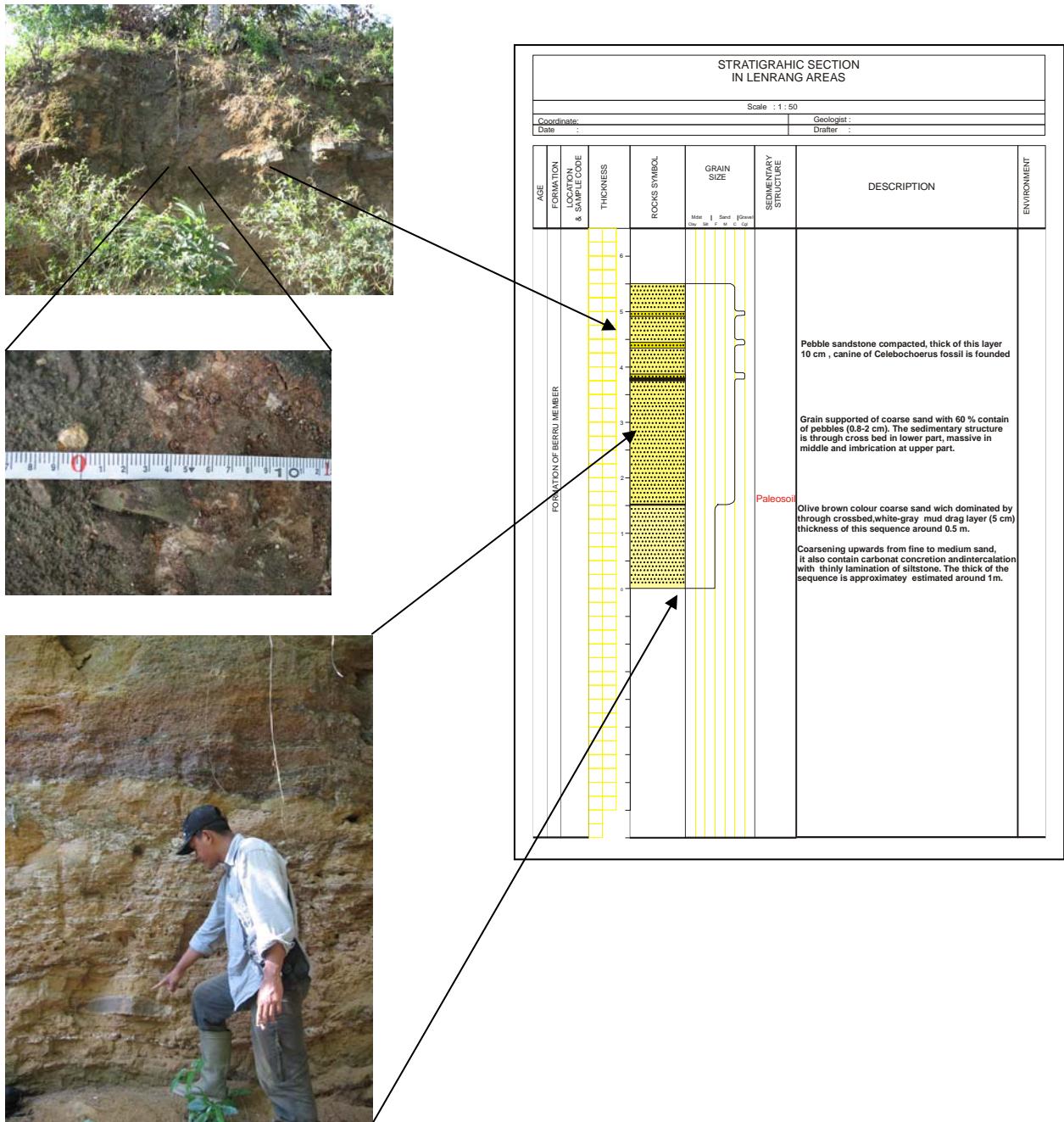


Fig.3-9. Detail stratigraphic section and plan of Beru Member is exposed at Lenrang. The *Celebochoerus* canine has been taken on compacted conglomerate at middle layer.

at Lenrang Village, in the southwest part of Sengkang Basin. The sequence is predominantly coarse grained sandstone, lags deposits, intercalated with compacted

conglomerate. The scoured base structure is dominant in this sequence; often ripple cross stratifications on medium to fine grained sand can be observed.

The detailed stratigraphic section shown in **Fig. 3-9** was taken by the author at a hill cut behind local houses. On the basis of composition, sedimentary structures, lateral accretion, and thin layers of fine grained deposit, the area was interpreted a point bar with occasional high energy transport, in the meandering system of Paleo Walanae River system.

Terraces

Old Alluvial Terrace deposits unconformably overlie the Beru Member at Talepu and Paroto Villages, both with *in situ* stone artefacts. The terrace fills consist of unconsolidated, subangular to sub - rounded fragments, some derived from the Walanae Formation, but also silicified limestone and chert pebbles. The matrix consists of coarse-grained sand. At Paroto a layer of these deposits, which contains stone artefacts, has been cemented by carbonate. The terrace deposits did not yield any fossil remains.

Van den Bergh (1999) also identified the Tanrung Formation, comprising cemented, terrestrial conglomerates, unconformably overlying the Walanae Formation in the East Sengkang Basin. Large - bodied *stegodon* maxilla fragment with dentition, as well as *Celebochoerus* remains, were found embedded in these conglomerates. The Tanrung Fauna is clearly different from that of the upper Walanae Formation. However, the boundary between the Tanrung and Walanae Formation is not clear. As the former is intensively weathered and is not represented in good outcrops.

Considering the distribution, limited thickness and low elevation, the Tanrung Formation can be best interpreted as a coastal terrace.

III.5. Conclusion

The tectonic history of Sulawesi, the Makassar Strait, Sulu Archipelago and Sunda from the Middle Eocene to the present provides a context for faunal dispersal to South Sulawesi. Over this time, there is no evidence that land bridges ever existed between Sunda and any part of Sulawesi. Animals colonising the island, therefore, had to make a sea crossing, which may have been much shorter during the Middle Miocene, when deltaic progradation on the east coast of Borneo extended further east than at present. This was the time when the ancestors of *Celebochoerus* may have colonised Sulawesi.

In the following Chapter Four, information on the taxonomy and phylogeny of extant and extinct suids, including *Celebochoerus*, will be summarised. This includes their diagnostic traits, habitat, ecology and adaptive morphology. I will then document and analyse recently collected *Celebochoerus* cranial remains and dentition. These new finds have some morphological traits not previously known for this fossil suid.

CHAPTER FOUR

THE TAXONOMY OF SUIDAE

IV.1. Introduction

This study focuses on the taxonomy and functional anatomy of *Celebochoerus*, an endemic fossil suid known from the Walanae Formation of the Sengkang Basin, Southwest Sulawesi. To put this species in context, however, I will begin with a summary of suid taxonomy.

The Suidae belong to the mammalian order Artiodactyla, the even-toed ungulates or Cloven-hoofed mammals (Thenius, 1970 vide Groves, 1981). The extant Artiodactyla are divided into three main lineages, generally ranked as suborders: Suina, Tylopoda and Ruminantia. These comprise, respectively, the pigs and their relatives: peccaries and hippos; the camels and lamas; and the true ruminants, such as cattle, sheep, goats, antelopes, deer and giraffes. There is still debate about the phylogenetic position of the hippos – traditionally considered as close relatives of the pigs. However, recent DNA studies and the fossil record, indicate that hippos are derived from the now extinct family, the Anthracotheridae, and are the closest living relatives of Cetacea - whales. This implies that the Artiodactyla are paraphyletic, because Cetacea are not included. Therefore, a new clade, the Cetartiodactyla has been proposed (Boisserie *et al.*, 2005).

In the Suina, there are two living families: Tayassuidae (peccaries) and Suidae (pigs). Both have a snout disc or rhinarium, a remarkable organ adapted to rooting in the soil. The peccaries comprise three extant species assigned to two genera, *Tayassu* and

Catagonus (i.e. *C. wagneri*). Peccaries first appeared in the Oligocene of Europe, but are now restricted to the Americas (Groves and Grub, 1993).

Suidae are characterized by medium-sized bodyweight; head long & pointed; snout used in digging with terminal cartilaginous disk pierced by nares and supported by unique rostral or prenasal bone; C1 rounded to triangular in cross-section, larger in males; canines directed outward & may curve dorsally; C1 abraded across tips (honed with c1); molars primitively brachydont & bunodont, but may be specialized for grinding abrasive grasses; 3rd molars primitive with small talon/talonid, but increased size in specialized grazers; tail short & thin, usually with terminal tuft of hair; epipodials thin; autopodia narrow, with four digits of which the two central digits bear flattened hooves & are used in normal locomotion; stomach simple except for cardiac pouch; dorsal anal gland absent; skin tough & thick ; 4+ mammary glands; hair coarse and sometimes sparse; often with knobs, warts & fenders on skull associated with male combat.

All Suidae have a snout disc, a unique character shared with the peccaries that separates them from all other Artiodactyla. Since this suborder is most relevant to the thesis topic more detail is given here on distribution, characteristics and phylogeny of the Suidae, which comprise three extant subfamilies, five genera and two tribes (**Fig.4.1**). In summary these comprise:

- Subfamily Babyrousinae
 - Genus *Babyrousa*
- Subfamily Phacochoerina
 - Genus *Phacochoerus*
- Subfamily Suinae
 - Tribe *Potamochoerini*
 - Genus *Hylochoerus*
 - Genus *Potamochoerus*
 - Tribe *Suini*
 - Genus *Sus*

(Photographs of the various pig species that accompany descriptions are all from <http://chasmosaurine.blogspot.com/2007/02/natural-history-of-pigs-part-ii-tusks.html>).

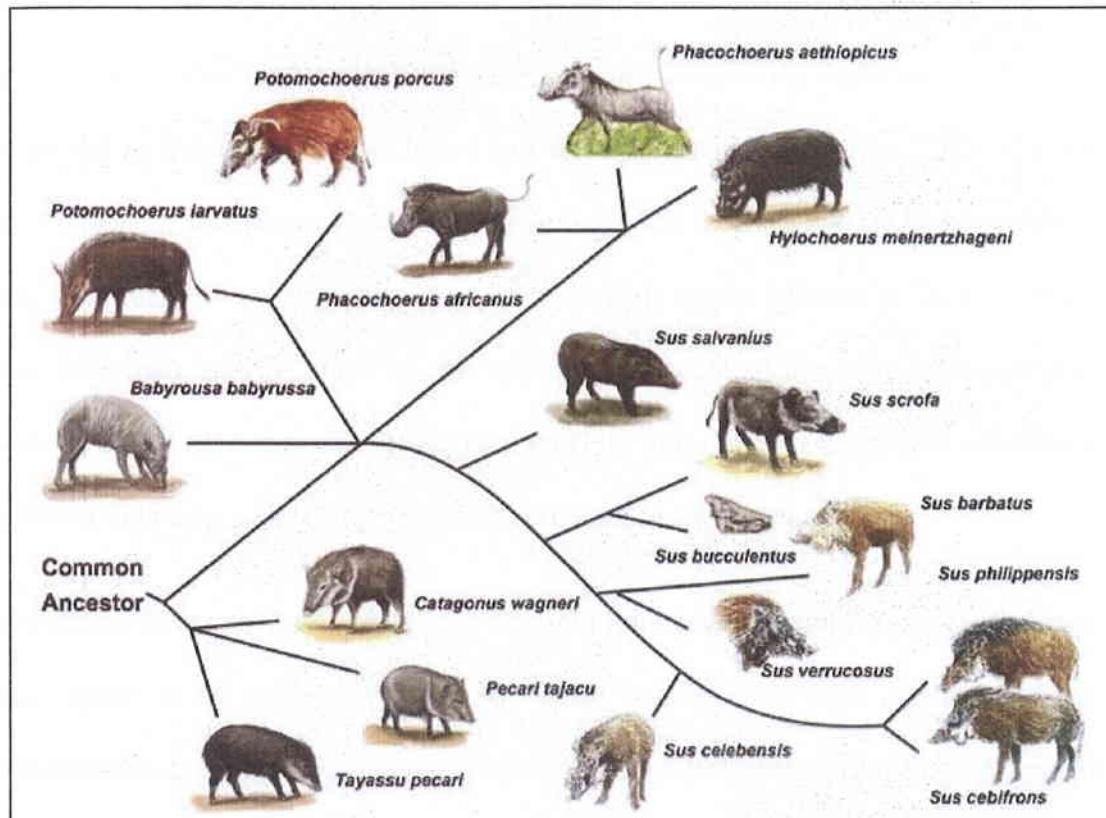


Fig. 4.1 the Suinae diversity and phylogenetic relationships (Chen et. al, 2007)

In addition, there are a number of extinct Suidae genera relevant to this study of *Celebochoerus*. These include *Propotamochoerus* from the Late Miocene of the Siwaliks in India and China; *Microstonyx* from the Lower Miocene of China, Europe and Africa, *Paleochoerus* from the Lower Miocene of the Indian Subcontinent, and *Kolpochoerus* from the late Miocene and Pliocene of Africa.

IV.2. Recent Suidae

IV.2.1. *Babyrousa* Perry, 1811

The Babyrousa or pig-deer is a very primitive pig species whose relationship to other members of the suid family is distant and poorly understood. There is one extant species in its own subfamily the Babyrousinae; *Babyrousa babyrussa*, which is restricted to Sulawesi, Buru, Togian and the Sulu Islands (Thenius, 1970; Groves 1981). Several subspecies are usually recognized, but recent work suggests that there may be actually three distinct species, differentiable on the basis of geography, body size, body hair and the shape of the upper canine tooth of the male (Meijaard and Groves, 2002). *B. babyrussa* also occurs on Buru and the Sula Islands, *B. celebensis* in North Sulawesi, and *B. togeanensis* is restricted to the Togean Islands.

In addition, Holocene fossil material from Bola Batu cave, around 20 km southwest of Watampone in the Bone district of Southwest Sulawesi has been attributed to the subspecies *B. babyrussa bolabatuensis* (Hooijer, 1950). Hooijer (1948) also proposed another subspecies, *Babyrousa babyrussa beruensis*, on the basis of four fossil molars collected by van Heekeren. However, he later reallocated these specimens to *Celebochoerus*. The primitive molars of these two pig types are very similar.

Diagnostic traits

Distinctive characteristics of *Babyrousa babyrussa* include the fact that the species is wrinkle-skinned, almost hairless and has relatively slender legs – in fact relatively longer than those of any other living suid (Aziz, 1990). Also the upper tusks, comprising the upper canines, grow upward instead of sideward, penetrating the skin of the snout, and then curving backwards. This anatomical trait is not found in any

of the snout, and then curving backwards. This anatomical trait is not found in any other known suid. Groves (1981) describes how the upper canines initially grow down in the alveolus. As the canines continue to grow the canine flanges rotate upwards and the canines start to pierce the skin of the snout, growing upwards and backward. Only males possess these large upper tusks, which may be up to 40 cm in length. They are brittle and used in sexual display and ritual combat rather than as a defence against predators. Similarly, the lower canines are only found fully developed in male adults. In females, they are either not present or reduced in size (**Plate 2, Appendix 6**).

Habitat, Ecology and Behaviour

Babyrousa babirussa lives in tropical rain forest on the banks of rivers and ponds abounding in water plants near coasts, as well as in lowland and mountain forests (Groves and Grubb, 1993). The species is omnivorous, and is known to consume leaves, roots, fruits, eggs and small animals. It is also social, usually occurring in groups of more than eight individuals.

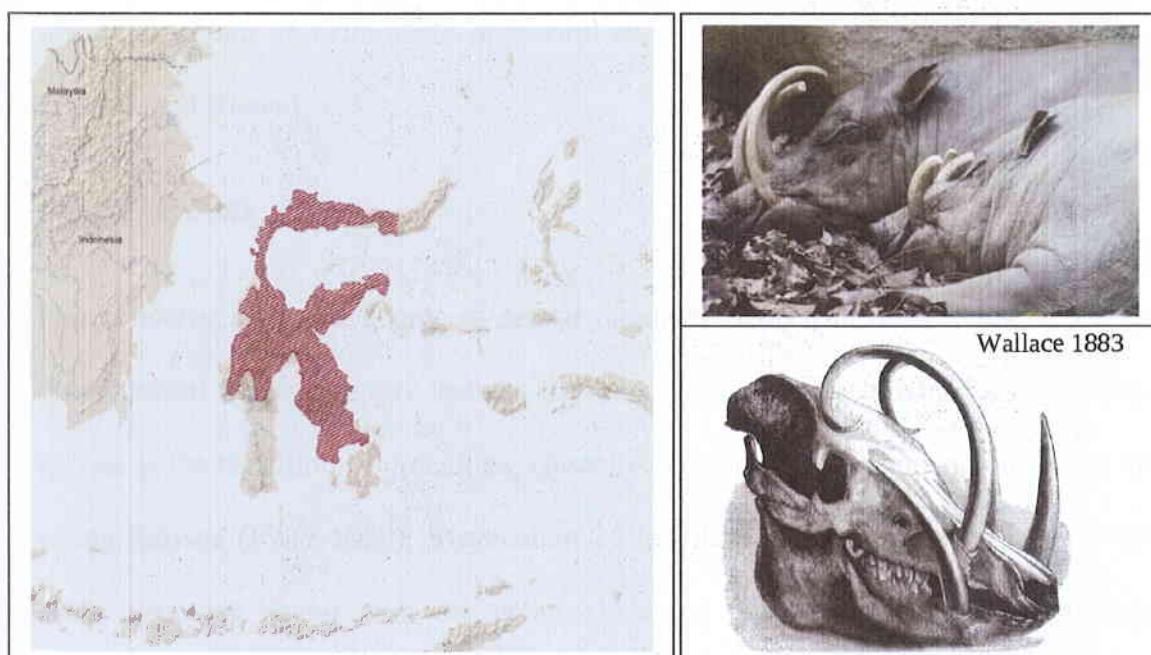


Fig.4.2 *Babyrousa babirussa* from Sulawesi and the Sula Islands and its current natural distribution
(Source map: www.iucnredlist.org, 2008).

Phylogeny

Babyrousa has a number of primitive characteristics shared with Oligocene pig species (Thenius 1970). The premolar and molar teeth have relatively simple cusp patterns, and unlike other extant pig species the snout is relatively short and not used for rooting. Canines lack enamel bands; the stomach is complex. More specifically, Groves (1976) suggest that the ancestor of *Babyrousa* should be sought among the fauna in the Siwaliks Hills of India.

IV.2.2. *Phacochoerus* Cuvier 1817, Warthog

Two extant species occur in genus *Phacochoerus* – *P. africanus*, or the common warthog, and *P. aethiopicus*, the desert warthog (Ewer 1958). The former still has a wide distribution throughout the savannah grasslands of Africa. However, of the two recognised subspecies of desert warthog, one became extinct in South Africa in 1865, while the second, *P. aethiopicus delamarei* survives in the Horn of Africa (Somalia, Ethiopia and Kenya).

Diagnostic traits

Phacochoerus lacks the degree of sexual dimorphism seen in other suids, and it is characterized by large upper canines in both sexes. A characteristic feature of the species is the reduction of premolars, typically an adaptation for grazing on the tip of young grasses (Ewer 1958). Mastication of the food then predominantly involves lateral chewing action with the greatly enlarged lower and upper third molars functioning as grinders. The third molars have progressively increased in size over time, an evolutionary feature that makes *Phacochoerus* very suitable for biostratigraphic purposes. Grazing also causes distinctive wear on the antero -external

time, an evolutionary feature that makes *Phacochoerus* very suitable for biostratigraphic purposes. Grazing also causes distinctive wear on the antero -external surfaces of canines, but in females, the upper canines are incurved towards the tips, out the way of the slicing lowers.



Fig.4.3. A lower jaw of *Metridiochoerus modestus* from the early Middle Pleistocene of Ethiopia. This extinct genus on the *Phacochoerus* lineage also has the enlarged M_3 adapted for grazing (Geraads et. al 2004).

Habitat, Ecology and Behaviour

Warthogs occupy a wide range of habitats, ranging from open, woodland savannah, grassy steppe and semi dessert, and higher topographic areas (e.g. Ethiopian plateau). They are predominantly grazers and also consume sedges, fallen fruits and certain forbs. According to Cumming (1975), they are mostly diurnal, sleep at night in burrows, and can tolerate significant fluctuations in body temperature.

In addition, warthog lower canines extend laterally and are clearly useful for defence against predators in open grassland. Inter-male fighting is by pushing with the

forehead until one animal gives way (Groves, 1981). Warthogs are usually solitary or travel in small groups and do not defend territory, but adult males fight for access to females. The common name warthog comes from the four large wart-like protrusions found on the head that serve a defensive purpose during inter-male fights. Warthogs are also characterised by a slight jerky movement of the head.

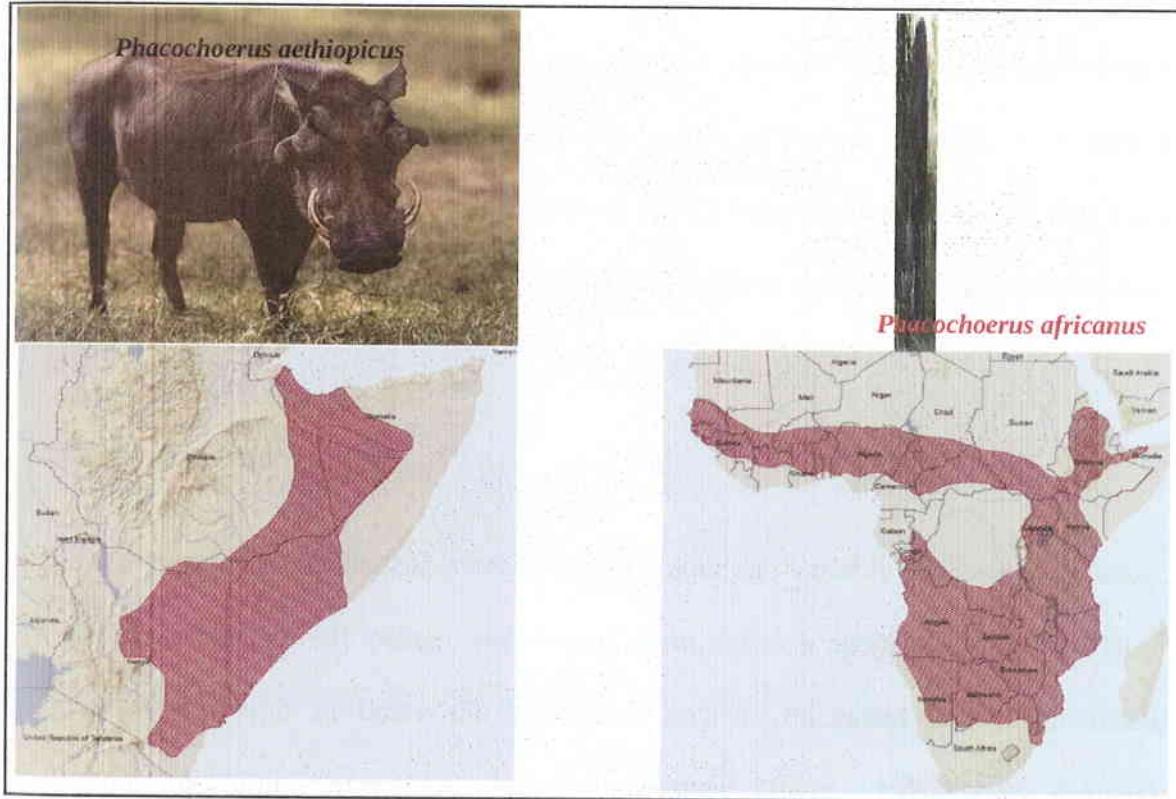


Fig.4.4 The current natural distribution of *Phacochoerus aethiopicus* (desert warthog) and *Phacochoerus africanus* (common warthog) (Source map: www.iucnredlist.org, 2008).

Phylogeny

Concerning ancestry, *Phacochoerus* has a number of characteristics found in pigs from the Middle Miocene Siwalik deposits of India. These early pigs include *Paleochoerus perimensis*; *P. lahirii* and *P. pommel*, which also had large upper canines, reduced first and second premolars, and a relatively short and rounded snout

radiation until some time in the Miocene. The ancestor of the *Phacochoerus* lineage first arrived in Africa from Eurasia during the Middle Pliocene, as represented by *Metridiochoerus* (Harris and Cerling, 2002).

IV.2.3. Genus *Hylochoerus* Thomas 1904, Giant Forest Hog

There is only one extant species in this genus, *Hylochoerus meinertzhageni*, which was first discovered in the Aberdare Mountains of Kenya in 1904. It is widely distributed throughout the central forests of Africa from Guinea via Gabon and Zaire to the mountains of Kenya, such as Aberdare, Mt Meru and Mt Kilimanjaro (Groves, 1981).

Diagnostic traits

Hylochoerus meinertzhageni is coal black in colour and variable in shape when adult. It has a wholly bristly pelage, very broad snout, no tusk apophyses, and no rostral warts - although in boars the zygomatic arch is thickened and pneumatised, supporting large infraorbital renoid swellings (Ewer, 1970 vide Groves). Characteristics differentiating the genus from *Potamochoerus* include the hypodont enamel pillars supported by cement, which wears through to the dentine soon after eruption. Furthermore, the facial musculature and the structure of skull are adapted to a herbivorous rather than an omnivorous diet. This genus overlaps in size with *Potamochoerus*.

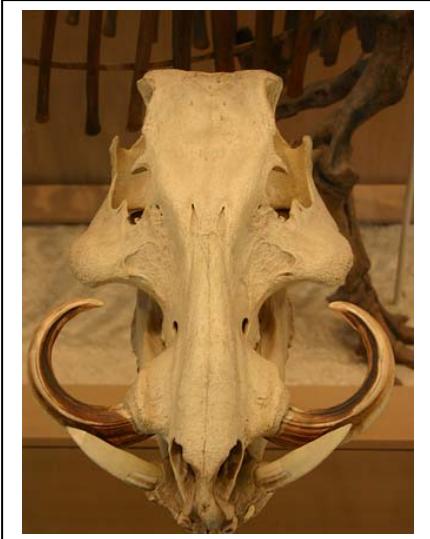


Fig.4.5. Frontal view of *Hylochoerus meinertzhageni* skull. Note the swelling on the jugal arches.

Habitat, Ecology and Behaviour

According to Haltenorth (1963) and Ansell (1972), there are three subspecies:

Hylochoerus meinertzhageni ivoriensis from Liberia, Ivory Coast, Ghana and Togo;

Hylochoerus meinertzhageni rimator (synonym with *ituriensis*, *giglioli*) from highland forests where in the Cameroon borders Nigeria, Congo and Zaire; and

Hylochoerus meinertzhageni meinertzhageni (synonym: *schultzi*) from eastern Zaire, Uganda, Kenya and Ethiopia, where the boundary between the lowland forest *H.m. rimator* and the large highland race most probably occurs along the foothills of the Rift Highlands (Cotton, 1936). The last mentioned subspecies has the greatest skull length for the genus - around 381-427 mm for females and 410-461 mm for males.

Phylogeny

The genus is almost not represented in the fossil record until the Late Pleistocene, when they are common at Gamble's Cave (Leakey, 1985). *Hylochoerus* is descended from, or an endemic derivative of, *Kolpochoerus* (synonym of *Mesochoerus*), a Late Pliocene to Middle Pleistocene pig genus, represented at Olduvai Gorge in the eastern Serengeti of northern Tanzania.

Pliocene to Middle Pleistocene pig genus, represented at Olduvai Gorge in the eastern Serengeti of northern Tanzania.

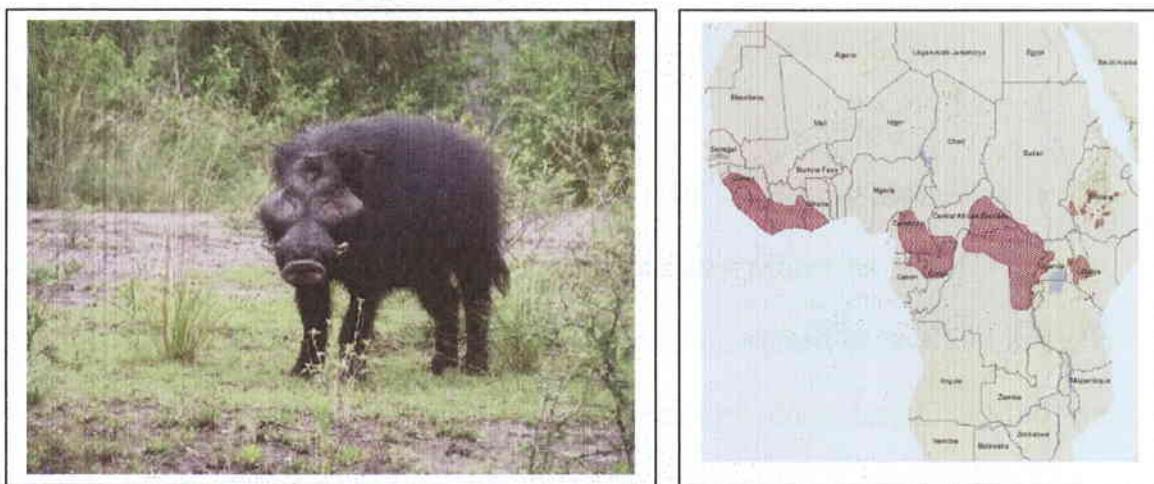


Fig.4.6. *Hylochoerus meinertzhageni* (giant forest hog) and its current native distribution
(Source map: www.iucnredlist.org, 2008)

IV.2.4. Genus *Sus*

Sus can be divided into various recent species on the basis of skull characters (Schwarz 1914 vide Groves, 1981), while traits of the lower canine of males help identify subspecies (Stehlin 1889 vide Hardjasasmita, 1983).

Estimates of the number of species vary, but in Indonesia there are at least five, more than in any other comparable area in the world - *Sus verrucosus*, *S. barbatus*, *S. scrofa*, *S. celebensis* and *S. papuensis*. However, the exact number of species and subspecies is still uncertain. Using molecular and morphometric techniques, Lucchini *et al* (2005) argue for two main *Sus* evolutionary clades that are likely to have diverged during the Pliocene: one includes wild pig populations now found in the Philippines (*Sus cebifrons*) and Sulawesi (*S. celebensis*); the other clade includes the Indonesian and Malaysian bearded pigs (*S. barbatus*), and the widespread Eurasian wild boar (*S. scrofa*).

Sus verrucosus Muller, 1840

Sus verrucosus, meaning ‘warty pig’ (or ‘babi kulit’ in Bahasa Indonesia), is now confined to Java and Bawean Island, but only became extinct on Madura recently. Two subspecies are recognized – *S. v. verrucosus* widespread in Java and formerly Madura, and *S. v. blouchi* now confined to Bawean. Body length: 90-190 cm; shoulder height: 70-90 cm and weight: 35-150 kg. The nominate form is much larger, with sample-means of greatest skull length 408-429 mm in males, whereas the Bawean race (Groves, 1981) has a skull length of only 354 mm.

Since 1996, the species has been classified as endangered by the International Union for Conservation Nature (IUCN).

Diagnostic traits

Sus verrucosus is, like *S. barbatus*, distinguished from other *Sus* species by an elongated facial skeleton; the depth and extent of the preorbital fossa; inflated molars; a broad, square and overhanging occipital; small rounded orbits; narrow, and generally bifid antorbital foramen; the diastema between upper canine and cheek teeth; and swelling of the mandible.

They also have a greater skull length than other species, as well as narrower and longer molars than *S. scrofa vittatus*. Externally, *S. verrucosus* pigs are also characterised by facial warts and cheek tufts (Schwarz, 1914 vide Groves, 1981).

There is marked sexual dimorphism in terms of body size in adults, with males being more than twice the weight of females: Female condylobasal skull length was only

80.3-83.3% of male measurements in two populations. The species is also relatively long limbed; with a large, heavy head compared to the body; a long straight back; six pairs of mammae; and a snout disc somewhat oblique to the axis of head. Three pairs of warts; the infraorbital pair are the largest; while a long tuft of hair on gonian marks the spot where a gonial wart will emerge late in life in males.

Habitat, Ecology and Behaviour

The species mainly occupies secondary or disturbed forest, and are also found near the coast in remnant patches of mangrove and swamp forest or in areas below 800 m in altitude. They are rare in lowland primary forests (Groves, 1993). Most births occur during the rain season months of January, February and March. The largest groups of Javanese warty pigs usually comprise four to six individuals.



Fig.4.7. *Sus verrucosus* (the Javanese warty pig) and its current natural distribution
(Source map: www.iucnredlist.org, 2008)

Sus barbatus Muller, 1838

S. barbatus is closely related to *S. verrucosus*, but is typically distinguished by the bushy gonial tuft of hair enlarged into a cheek-beard, much smaller warts and a still more elongated skull.

Formerly, the bearded pig, or *Sus barbatus* occurred in Sumatera. From there, it has spread widely into Sundaland, including the Malay Peninsular, Borneo and Palawan (Gibson-Hill, 1950; Headway, 1978; Groves, 1981).

There are three currently recognized subspecies: 1) *S.b. oi*, in peninsular (West) Malaysia, Sumatera, Bangka and Pulau Bintang in the Riau Archipelago; 2) *S.b. barbatus* in Borneo and the westernmost of the Sulu Archipelago; and 3) *S.b. ahoenobarbus* in Balabac, Palawan and offshore islands. The subspecies differ in size, coloration and hair development. The nominate race of Borneo is large, with a well-developed beard, while *S. b. oi* is somewhat variable over its disjunctive range, but is also very large, has coarse bushy hair over the top of the snout and a smaller beard. *S. b. ahoenobarbus* is much smaller and darker. Sample-means of greatest length of skull in males are 359-365 mm, against 435-505 mm in the larger races.

In the Philippine archipelago, *Sus philippensis* and *Sus cebifrons* have generally been assigned to the species *Sus celebensis* (Sanborn, 1952). However, Groves (1981) rejected this arrangement on finding that their cranial characters aligned them with *S. barbatus* and not *S. celebensis* - a view subsequently endorsed by Mudar (1986) – whilst acknowledging that they might merit separation as full species. It now seems

appropriate to distinguish two separate species on the Philippines (excluding the Palawan Region), namely *S. philippensis* and *S. cebifrons*.

Diagnostic traits

The characteristics of this species are a relatively large body size, a strong degree of sexual dimorphism, condylobasal skull length of females 88.2- 93.6% of males, an elongate skull (even more so than in *Sus verrucosus*), long legs, a bearded jaw (genial tuft) and sparse body hair (Pfeffer, 1959 vide Groves).

Habitat, Ecology and Behaviour

Naturally, the bearded pigs occur in tropical evergreen rainforest, but they can also live in a wide variety of environments from beaches to highlands to upper closed mountain forest. Bearded pigs are omnivorous rather than herbivorous; they eat roots, fungi, tropical fruits, small vertebrates and eggs.

The carrying capacity for bearded pigs no doubt varies greatly from habitat to habitat within the rainforest. Population density is also radically variable over time (Caldecott et al., 1993). Fruit supply is believed to have particular influence in determining growth rate, fat deposition and reproduction, with the oil-rich seeds of members of the tree families Fagaceae (oaks and chestnuts) and Dipterocarpaceae (dipterocarps) being especially important in this regard

According to Pfeffer (1959), *Sus barbatus* moves consistently in one direction, in scattered or condensed herds, over period of several days, weeks or months. The animals are also seen regularly swimming across rivers, sometimes coastal bays and even out in open sea. Additionally, *Sus* migrations were recorded by Davies and Payne (1982) over distances more than ten kilometres in Sabah. The approximate

Payne (1982) over distances more than ten kilometres in Sabah. The approximate travel rate during mass movement given by Caldecott (1988a) is 8-22 km/month. Pfeffer (1959) suggest rates of pig migration involving distances unidirectional movements of 250-650 km.



Fig.4.8. *Sus barbatus* (the bearded pig from Borneo) and its current natural distribution
(Source map: www.iucnredlist.org, 2008)

Sus scrofa Linnaeus, 1758

Sus scrofa or the Eurasia wild pigs first appeared in western European and from there moved to North Africa and the Asian mainland, arriving in Java and Sumatera in the Holocene. *Sus scrofa* can be subdivided into several subspecies, which are moderate to large in size with a fairly short muzzle and no face warts. In Indonesia, the subspecies of *Sus scrofa* is *Sus scrofa vittatus*, which was widely distributed as far east as Bali. Since Neolithic times, domesticated pigs have been carried across water barrier into the islands of Eastern Indonesia, establishing feral populations in many

places. *S. scrofa vittatus* is characterized by body hair space, no under wool, with skull lengths of males around 284-380 mm (Groves, 1981).

Diagnostic traits

Pigs of the *scrofa* group are characterized by the absence of warts or genial whorls, relatively large ears, long limbs, and a relative small head compared to body size. Females are 88.8 – 95.3 % of male in condylobasal length in various populations (Groves, 1981, while the length of skull of males varies between 275 mm (Ryukyu Islands) and 466 mm (Ukraine). Domesticated pigs are derived from *S. scrofa*.

Habitat, Ecology and Behaviour

Naturally, the Eurasian wild pig occupies a wide variety of habitats including tropical evergreen rainforest, semi desert, temperate woodland, grassland, and reed jungles. Furthermore, these pigs are omnivorous rather than folivorous, i.e. roots, fungi, tropical fruits, seeds, small vertebrate and eggs constitute 90% of the diet (Spitz, 1986). In behaviour, the wild pigs are normally most active in early morning and late afternoon, but can become nocturnal in disturbed areas.



Fig.4.9. *Sus scrofa* (Eurasian wild pig)

***Sus celebensis* Muller & Schlegel, 1845**

Sus celebensis, or the Sulawesi warty pig, is confined to Sulawesi and the surrounding islands of Selayar, Buton, Muna, Peleng, Lembeh and the Togian group. Feral populations also occur in the Moluccas, the Lesser Sundas and in the west Sumatera Islands of Simaleue and Nias (Groves, 1983; Bell, 1987). Evidence from the archaeological site Liang Bua in western Flores has shown that *Sus celebensis* was introduced in Flores some 7000 years BP, and that *Sus scrofa* was not introduced until the Neolithic around 4000 years ago (van den Bergh *et al.*, 2009).

Diagnostic traits

They are characterized by a clear yellow snout band, along with a distinctive tuft or crest of longer hair on the oldest adult. Adult males have three pairs of facial warts: the preorbital pair is the largest, the infraorbital smaller and the mandible warts emerge from a whorl of hair marking their position (Groves, 1981 and Hardjasasmita, 1987).

Part of a fossil *Sus celebensis* maxilla was collected from the bed of the Salo-Patjiro River between Pampanua and Soppeng, South Sulawesi. It consists of the palate with P^3 and M^3 on the left side and P^4 until M^3 on the right. On the basis of upper tooth morphology, there are no major differences between the fossil specimen, which appears to be of Middle Pleistocene age, and the extant species *S. celebensis*, except that teeth seem to have increased in size (Hooijer, 1969).

Habitat, Ecology and Behaviour

Sus celebensis occupies a wide range of habitats, including rainforest, swamp, woodland savannah, agriculture areas and higher topographic areas, in all altitudes up

to moss forest at 2,500 m asl (MacKinnon, 1981). Most births occur late in the rainy season months of April or May. They usually live in groups but the social behaviour is poorly known.

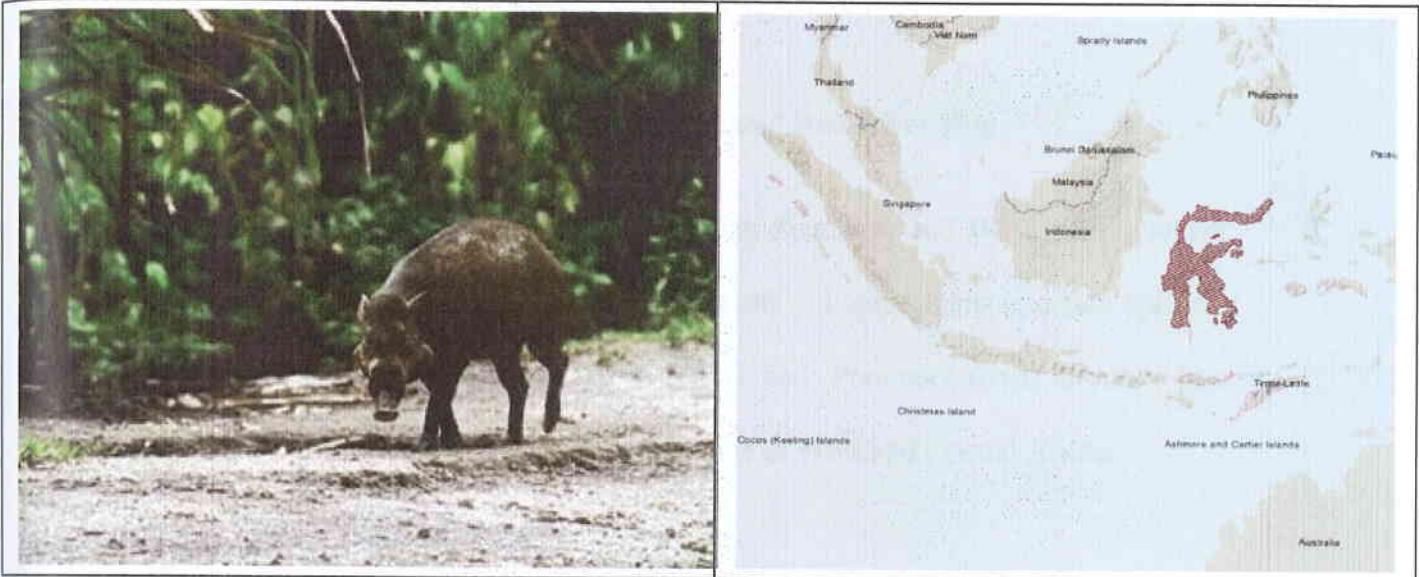


Fig. 4.10. *Sus celebensis* (Sulawesi warty pig) and current distribution. Its native distribution is shown in red hatching, areas where it has been introduced in the past and now lives as feral populations is indicated with pink hatching (Source map: www.iucnredlist.org, 2008)

In addition, Sulawesi warty pigs are omnivorous rather than herbivorous, i.e. roots, fungi, tropical fruits, leaves, small vertebrate and eggs make up most of the diet. They are normally most active in early morning and late afternoon, sometimes they became nocturnal in disturbed areas

Phylogeny of genus *Sus*

Sus can be separated from all other genera on the basis of the lower premolar characteristics. These pigs appear in the Lower Pliocene of Europe (*S. minor*) and the Bumiayu fauna, in Indonesia (*S. stremmi*), and are also found in upper Pliocene deposits in Algeria (*S. phacotherioides*), where they continue until the appearance of

scrofa in the Pleistocene. Concerning ancestry, fossils of *Sus* have characteristics shared with the modern representatives of the genus. The earliest species of *Sus* show a *verrucosic* type of cross section in the male lower canines, but this evolves over time into the *scrofic* type.

IV.2.5. *Potamochoerus* Gray 1854, Bush pigs and Red River Hog

Suids of the genus *Potamochoerus* are found in Southeast and West Africa, where they live in both bushland and forest. Mohr (1960) divided them into two species: *Potamochoerus porcus* (the Red River Hog) and *Potamochoerus larvatus* (the Bushpigs). The Red River Hog replaces Bushpigs in West and Central Africa.

Diagnostic traits

Groves notes that distinctive characteristics of Bushpigs include a flattened nasal on the dorsal surface and overhanging slightly hollowed lateral rostral walls; the canine apophyses are enlarged and roughened and may nearly reach the nasal margin; and the premolars are flat and cuspidate on their occlusal surface, as opposed to the high cutting blades in *Sus*.

The three main masticatory muscles in *Potamochoerus* are larger than in all suidae except *Babirusa*. Interestingly, in *Phacochoerus* and *Hylaochoerus* these muscles are less enlarged, the whole snout is less mobile and the muscular insertions are less demarcated. The canine of both Bushpigs and *Sus* is similar, the uppers grind against the lowers, so that the latter are kept sharp while the former are rounded (Mohr, 1960).

Habitat, Ecology and Behaviour

These suidae live in a wide range of habitats including lowland forest, mountain forest, gallery forest, dry forest and savannah woodland. Both species are predominantly nocturnal (Seydack 1990).

Furthermore, they are omnivorous rather than folivorous, i.e. they eat roots, fungi, tropical fruits, small vertebrates and eggs. A field study by Ghiglieri, et.al (1982), showed that the species is often associated with groups of foraging monkeys in order to feed on discarded fruits.

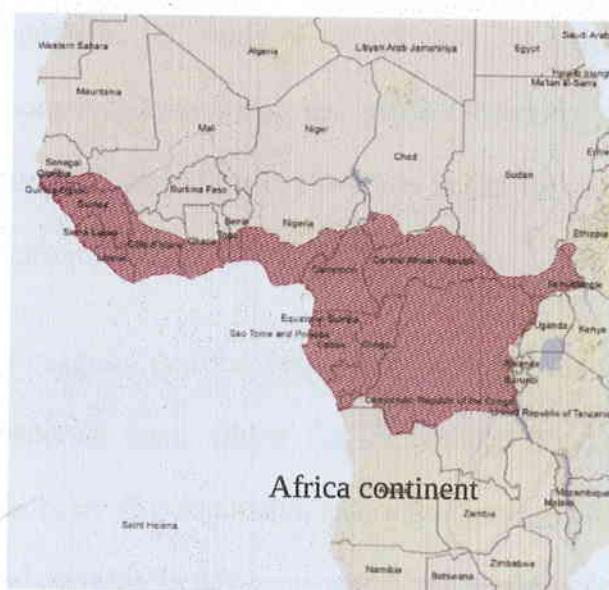


Fig.4.11. *Potamochoerus porcus* (Red River Hog) and its current natural distribution
(Source map: www.iucnredlist.org, 2008)

Phylogeny

Fossils of *Potamochoerus* are known from the Tatrot Plateau, in the lower part of the Pinjor Horizon (Middle to Upper Pliocene) of the Siwaliks, India. Fossil mandibles

Potamochoerus (Pilgrim, 1926). Concerning ancestry, this genus has a number of characteristics shared with *Propotamochoerus* (Miocene pigs) in the Siwaliks, India. Fossil bush pigs are also found in Late Pliocene to Middle Pleistocene deposits at Kubi Alga and Omo Shungura in East Africa (Harris and White, 1979). These pigs apparently migrated into Africa during the Late Pliocene.

IV.3. Extinct Suidae

Of particular interest for this study on the taxonomy of *Celebochoerus* are the fossils of genus *Propotamochoerus* from the Middle Siwaliks of India, and those of *Microstonyx* found in Lower Miocene deposits in Europe, Africa and China (van Der Made, 1999; Pickford, 2001).

Thenius (1970) suggests that the earliest Suidae from the Oligocene belong to the genus *Palaeochoerus*, from which the *Babyrousa* lineage may have separated. However, on the basis of comparative anatomy, Groves (1981), has argued that pigs appeared during the Middle Miocene within the Potamochoerini and Suini Tribes, with the genera *Propotamochoerus* and *Dicoryphochoerus*, which are present in the Middle Siwaliks. Other fossil genera are known from Africa: *Kolpochoerus* (previously called *Mesochoerus*) is derived from the *Propotamochoerus* stem and can be considered as the ancestor of *Hylochoerus*. According to White and Harris (1977) the Late Pliocene genera *Metridiochoerus* (synonym with *Stylochoerus*) in an ancestor of *Phacochoerus*.

In Indonesia, the earliest known fossil suid is *Sus stremmi* from Bumiayu in Central Java (von Koenigswald 1933). This evidence, comprising three premolars, a third

upper molar and two lower canines (now in the GSI Museum collections), comes from the Upper Kaliglagah Beds, which are between 1.5 and 1.2 million years old, and is associated with the Ci Saat Fauna (Sondaar et.al, 1984 and van den Bergh 1999),

Other fossils suid species described from the Pleistocene of Java are *Sus brachygnathus* from Trinil with an age of 0.9 Ma, and *Sus macrognathus* from the Kedung Brubus and Ngandong, with ages of 0.7-0.8 Ma and Late Pleistocene, respectively. These fossils provide crucial evidence the phylogeny of extant and extinct suid genera, but do not appear to be closely related to *Celebochoerus*.

IV.4. Genus *Celebochoerus*

Celebochoerus fossil were first described in the late 1940s by H. R. van Heekeren. The fossils came from Sompoh in the Tjabenge area, Soppeng District, and comprised two fragmentary, large upper canine fragments that were attributed by Hooijer (1948) to a new genus and species, *Celebochoerus heekereni*, described as a giant Suidae with upper tusks subtriangular in cross section and with the posterior surface wider than the anterior surface. Since the initial discoveries, much more material has been found, including crania, teeth and postcranial elements.

Diagnostic traits

In Suidae, the (male) lower canines are divided into two types, *scrofa* and *verrucosic*, based on the ratio between the posterior and external surface. In the *verrucosic* type, the posterior surface is narrower than the external one, while in *scrofa* type pig the

posterior surface is wider than external. In the case of *Celebochoerus*, the lower canines are of *verrucosic* type.

Hooijer (1948a) initially believed that there was no coated enamel band developed on the upper canines. However, when more upper canines had become available to him, he then noticed that some upper canines do have an enamel band while others do not (Hooijer, 1954). If there is an enamel band developed, such as in *Sus* or *Potamochoerus*, then these are of variable width and found on the anterior edge of the lower surface. He distinguished between male and female canines, noting that from twenty-three specimens, seven upper canines were presumably female based on their more slender shape and smaller size. The presence or absence of enamel bands was not considered a distinctive character between males and females.

Hooijer also observed that the crania of *Celebochoerus* have an amalgam of anatomical traits observed in the other suid genera. The anteriorly placed zygomatic process of the maxillary, for instance, is a trait shared with the fossil genus *Propotamochoerus*, while the, nasal regions and the canine alveolus are similar to those of the extant *Phacochoerus*.

The notion of possible sexual dimorphism in canine size was based on fossil specimens from various localities, of which the relative and absolute age differences were not known at that time (Hooijer 1954). However, our more recent collection of *Celebochoerus* fossil canines is much larger, and includes many finds from two excavated localities, with widely differing average sizes. This will enable to test Hooijer's hypothesis of sexual size differences within *Celebochoerus*.

Habitat, Ecology and Behaviour

Evidence for the habitat and ecology of *Celebochoerus* will be summarised in Chapter Six, on the basis of the reconstruction of the paleoenvironment of the upper part of Walanae Formation (Late Pliocene to Early Pleistocene) by means of sedimentological and palynological evidence.

Phylogeny

A curious point arises here; *Celebochoerus heekereni*, was not ancestral to either of the two extant suid species on Sulawesi - i.e. *Babyrousa babyrussa* and *Sus celebensis*. This study will now report the results of my comparative study of the skull and dentition of *Celebochoerus heekereni* in the context of *Babyrousa babyrussa*, *Sus* and other extinct and extant Suidae genera from other regions (see Chapter V).



Fig. 4.12. Reconstruction of *Celebochoerus heekereni* (Drawing: Hans Brinkerink)

VI.4. Conclusions

In this chapter, I have presented evidence for the diagnostic anatomical traits of various pig taxa, as well as their phylogeny, distribution, habitat, ecology and behavior. These include a number of extant and extinct genera relevant to the evolutionary and biogeographic history of *Celebochoerus*.

In the following Chapter Five, I will present new qualitative and quantitative data on the skulls, canines, teeth and mandibles of fossil *Celebochoerus* remains held in the GSI Museum collections in Bandung, and assess this evidence in the context of comparative data from other extant and extinct suids. The aim is to reconstruct the phylogeny, history of dispersal and paleo-ecology of *Celebochoerus*.

CHAPTER FIVE

NEW FOSSIL SUID MATERIAL FROM SOUTH SULAWESI

V.1. Introduction

Evidence from Asia generally indicates substantial faunal immigrations into the region occurred during the Late Miocene to Pleistocene, and that local evolutionary developments also occurred. However, the contemporary fossil record for the Indonesian Archipelago is extremely scanty and mainly comes from Java. Shedding light on the biogeographic and evolutionary history of *Celebochoerus* known from Upper Pliocene and Lower Pleistocene deposits in SW Sulawesi, therefore requires morphological comparisons with other fossil, as well as extant suids from Eurasia and Africa.

As noted in the previous chapter, Hooijer (1954) considered *Celebochoerus* as derived from the same ancestral lineage as *Propotamochoerus*, but with an independent evolution since the Miocene: *Celebochoerus* retained the generalized molar structure of early Suidae but also developed specialized traits, including an increase in size of the upper canines at the same time as the anterior premolars reduced in size. The same advanced characteristics only evolved in one other lineage - that leading to the recent warthog, *Phacochoerus*.

For his seminal work on *Celebochoerus*, Hooijer (1954, 1972) only had access to skull fragments, which lacked parietal and occipital regions. However, since 1980 many more relevant fossils have been collected in Southwest Sulawesi, and these include skull fragments, teeth, and postcranials. These were obtained during field

campaigns in 1985-1990 (Aziz, 1990), 1989-1993 (van den Bergh, 1999) and 2007-2008, and they include relatively large fossil assemblages obtained by excavation at single locales.

The range of new fossils, now housed in the Geological Survey Institute (GSI) collections, provides important evidence for the anatomy, morphology, habits and habitats of *Celebochoerus*, as well as a much better basis for reconstructing the phylogeny of the genus, and identifying the ancestral lineage in mainland Asia, possible migration routes, and the timing of *Celebochoerus* extinction. Even so, the new fossil material has never been adequately described.

For this thesis study, I have focused on describing and measuring the new cranial and dental remains and analysis of the postcranial elements will be the subject of continuing research. In addition, I have made use of comparative data (as published or from my own work) on extant suid genera, such as *Babyrousa*, *Sus scrofa*, and *Sus barbatus*, and on extinct genera, such as *Propotamochoerus* from the Siwaliks in the Indian subcontinent and *Microstonyx* from China and Europe. Details on this comparative material are provided below and in Appendix A.

V.2. *Celebochoerus heekereni* Hooijer 1948

Family: Suidae Gray, 1921 (vide McKenna & Bell, 1997)

Genus: *Celebochoerus* Hooijer, 1948

Synonyms: *Babyrousa babyrussa beruensis* Hooijer 1948

Holotype: Basal portion of left upper canine figured in Hooijer (1948a, figs. 1-3).

Localities: Remains of *Celebochoerus* have been found near the following places and villages - Sombo, Beru, Celeko, Calio, Lonrong, Sare Batue, Paroto, Palangiseng, Marale and Bulu Cepo; and near the Lakibong and Tanrung Rivers. Except for the Tanrung River sites, all relevant fossil sites occur in the West Sengkang Basin. Most *Celebochoerus* fossils came from the Beru Member of the Walanae Formation (van den Bergh, 1999), but a few originate from the younger Tanrung Formation, which unconformably overlies marine deposits of the Walanae Formation in the East Sengkang Basin.

Age: The Beru Member is Late Pliocene in age with a lower boundary dated at 2.5 Ma, and the upper part presumably continuing into the Early Pleistocene. The age of the Tanrung Formation is not known with certainty, but is estimated to be Middle Pleistocene (van den Bergh 1999).

Diagnosis: see Hooijer, 1954

Amended diagnosis: U-shaped mandibular symphysis, Wide fronto-parietal area of the skull, with well-developed sagittal crest, and strong temporal ridges, upper part of occipital area slightly concave and wide, lachrymal arch weakly developed, lachrymal-maxilla-zygomatic junction flat or slightly convex, lacking concave pre-orbital fossa for attachment of the *levator rostri* muscles.

The Skull

A *Celebochoerus* skull fragment (GSI No. PR3145), surface collected at Paroto in 1993, is from a small adult. It is incomplete and heavily damaged along the left side (**Fig. 5-1**): the nasals and premaxilla are broken in front of the canine alveoli, the

canines are lost, and most dentition elements are broken. However, the outlines of the dental root masses can still be observed. Only the right P^3 is preserved, though heavily worn. Despite the small size, the skull must have belonged to an adult individual, because the M^3 was erupted and the P^3 is heavily worn. The skull fragment has been compressed post-mortem in a transverse direction, in particular the muzzle. The base of the right zygomatic arch of the maxilla is preserved, including the lachrymal and orbital rim. On the dorsal surface, the fronto-nasal area is rather damaged, showing various post-mortem pits filled with sandstone, which has obliterated the detailed structure of the suture lines. Only the suture between maxilla and nasals is clearly visible.

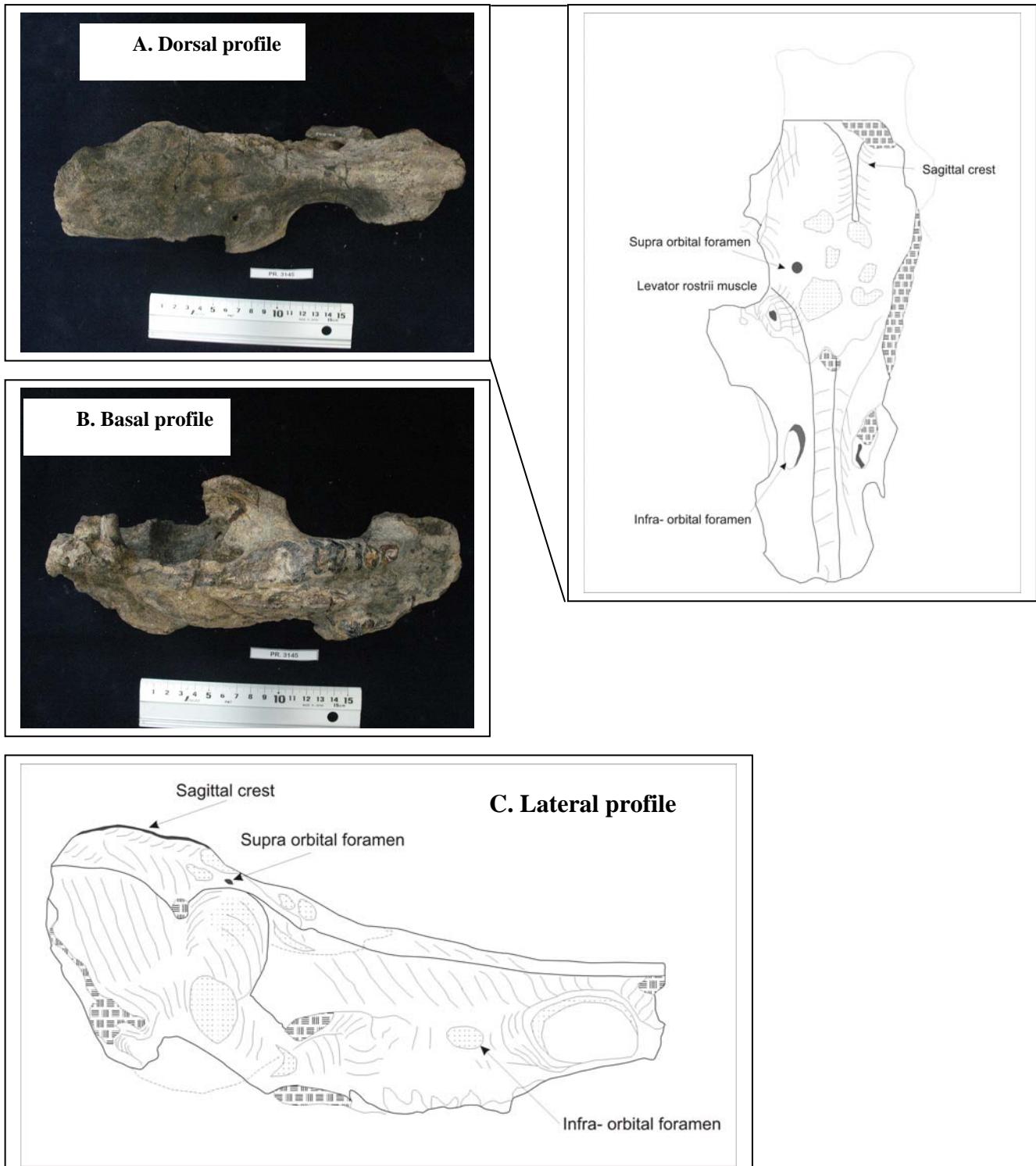
The occipital region is missing, but the dorsal surface of the fronto-parietal plane is largely preserved, on the left side including the dorsal border of the eye -socket and a large upper portion of the temporal region. The basic cranium is lost for the biggest part, only the left glenoid and the roof of the brain cavity remains, and the latter is filled with a hard sandstone matrix. However, this skull fragment is more complete than any previously described. In particular, the fronto-parietal region reveals some characteristics not recorded previously in *Celebochoerus*.

The nasal region is elongate and slender. The upper canine alveoli are dorsoventrally compressed, giving an ovaloid outline, but with the lower margin rather straight. The diameter of the right canine alveolus measures 35 mm in antero-posterior direction, and 24 mm in dorsoventral direction.

The canines projected laterally from strongly developed tubular alveoli. As with the maxilla fragments previously described by Hooijer (1972), the canine alveoli lack the dorsal bony ridge, or *jugum caninum*, which is developed in *Sus* and functions as a

guiding groove for the *levator rostri* muscles. The outline of the canine alveolus of *Celebochoerus* is similar to that of *Phacochoerus* rather than other suid genera.

Figure 5-1. A *Celebochoerus* skull surface collected near Paroto Village (GSI No PR3145).



The onset of the zygomatic process of the maxilla shows a remarkable abruptness, much like that seen in *Potamochoerus* and unlike the more streamlined profile seen in *Sus*. In dorsal view, the anterior margin of the zygomatic arch, or facial crest, forms an angle with the sagittal plane around 100° - 110° in *Celebochoerus* ((Hooijer 1972, measured around 100° ; see also **Fig. 6-1**). Actually, the facial crest extends laterally from the longitudinal skull profile nearly perpendicular, whereas the facial crest in *Sus* points more backward with an angle of between 135° - 140° .

The right jugal, as far as it is preserved, is heavily built and robust. The lachrymal is convex and lacks a distinct ridge above. The well-defined concave preorbital fossa (the origin of the *levator rostri*) in *Sus* and *Potamochoerus* is lacking in the fossil species, and there are no ridges marking the preorbital fossa off from the frontals and nasals. In *Babyroussa* the slightly concave preorbital fossa is rather intermediate between *Celebochoerus* and *Sus*, though a weakly developed crest above clearly marks off the boundary with the frontals and nasals.

The lachrymals and adjacent portions of the naso-frontal region merge gradually into each other without sharp edges, forming a rather bulging and convex cross section in the Paroto skull. As noted by Hooijer (1954), the lack of angulation in the muzzle and the poorly defined lachrymal fossa can also be observed in a poorly preserved *Celebochoerus* skull fragment from Sompe Village. In *Sus* and *Babyroussa* on the contrary, the flat frontals and nasals are bordered by sharp edges and drop off abruptly towards the lachrymal and lateral sides of the maxilla.

The right lachrymal foramen, with a diameter of 4.5 mm, is contained within a shallow depression approximately 16 mm long and 9 mm wide, and located at 12 mm from the orbital rim.

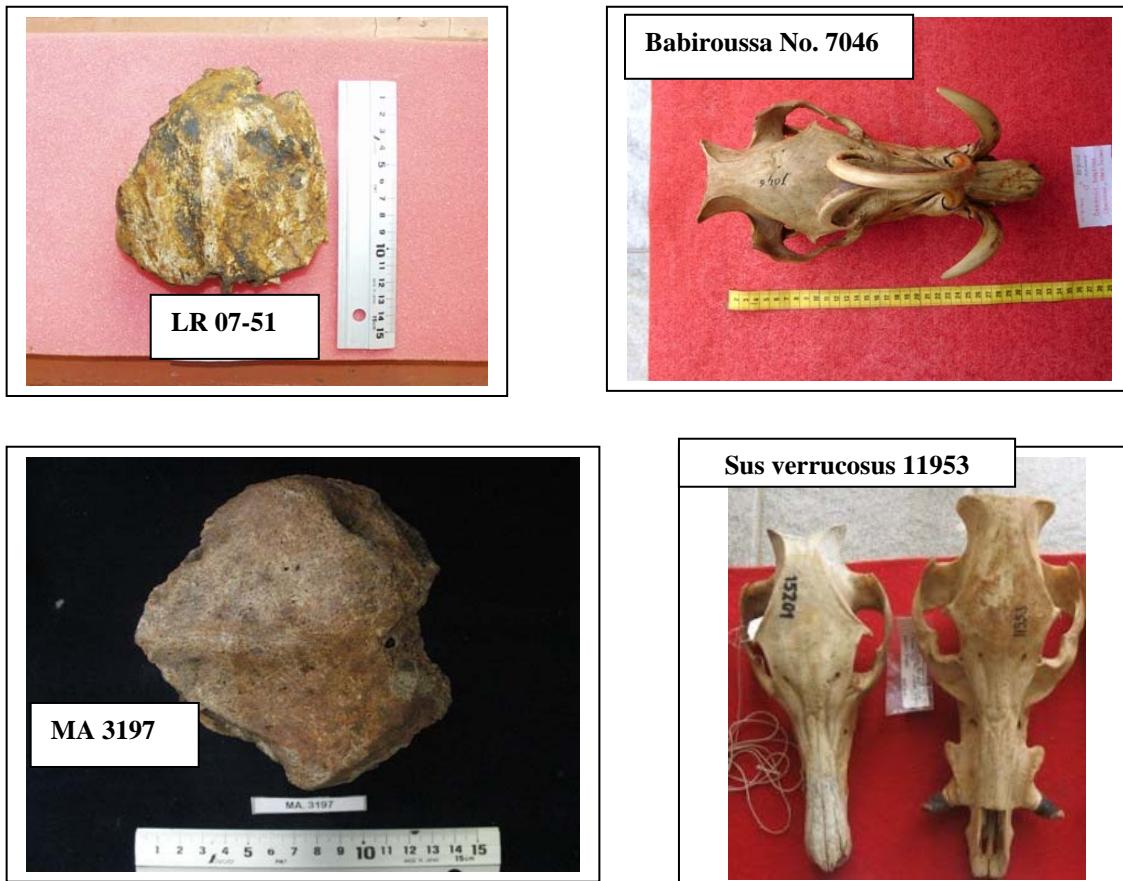
Due to the superficial damage of the frontals, the position of the supraorbital foramina cannot be distinguished. The fronto-parietal region is characterized by a well-developed sagittal crest, not found in *Sus* or *Babyroussa*. This crest is also well developed in three other *Celebochoerus* skull fragments (see below). The fronto-parietal plane is further characterized by its relatively large width between the temporal fossa, much wider than in *Sus* or *Babyroussa*. In the Paroto skull the left parietal is incomplete, but on the right side the minimum transverse width between middle of the sagittal crest and temporal crest amounts to 29 mm (measured parallel to the occlusal plane). The total minimum parietal width (measurement D3; see **Fig. 2-2**) would thus be about, 58 mm. In **Table 8** this measurement is also given for other suid species. In the Paroto skull the width between the slightly damaged postorbital process of the frontal and the sagittal crest measure 39 mm, giving a postorbital width of at least 78+ mm (measurement D8). Despite the slight post-mortem compression of the skull, it is clear that the fronto-parietal width between the temporal fossa in *Celebochoerus* was much wider than in *Sus* and *Babyroussa*. In lateral profile, the dorsal skull surface is concave along its entire length (**Fig. 5-1C**). In *Babyroussa* and *Sus*, the dorsal surface is almost straight and the fronto-parietal plane merges more gradually into the nasal plane (**Fig. 5-2 below**).

There are several other *Celebochoerus* skull fragments that were excavated at Lonrong. Specimen GSI No LR07-51 is a frontal skull fragment (**Fig.5-2B**) that also shows a well developed sagittal crest and relatively wide fronto-parietal plane, with a minimum transverse width of 104.8+ mm as far as preserved.

Figure.5-2 A. Several recent suidae skulls in lateral profile. Top left: female *Babyroussa* skull (coll. Mus.Bog. 15201), Top right male *Babyroussa* skull (coll. Mus.Bog. 7046).



Figure.5-2 B. The parietal crest on *Celebochoerus* skulls fragments from Lonrong (LR 07-51 top left) and Marale (MA 3197, bottom left) is more developed than for any extant genera. Top right: male Babyroussa skull (coll. Mus.Bog. 7046, male); Bottom right male and female *Sus verrucosus* (coll. Mus.Bog.11953 male and 15201, female).



Of comparable proportion is a fronto-parietal skull fragment that was surface collected near Marale Village (GSI No MA-3197; **fig.5-2B**). The fragment includes a large portion of both temporal crests, on the right side preserved slightly further forward than on the left side, and the upper region of the anterior parts of the temporal fossa. The supra occipital is largely broken, and anteriorly nothing of the eye sockets remains. The roof of the braincase is preserved and the fragment shows nicely in cross-section that the pneumatic cavities, as well as the braincavity, are filled with hard sandstone matrix. The fronto-parietal suture is fully fused in this specimen, and the fragment clearly belonged to an adult individual. This skull fragment also has a well developed sagittal crest, which is elevated 7 mm above the adjacent frontal plane. The crest rapidly fades out near the back, just in front of the parietal area, which bends slightly downward (the parietal plane its self is largely broken). In transverse cross section the sagittal crest is sharp, but with a wide base that merges gradually into very weakly concave frontal planes on both sides. The frontals on both side terminates laterally in convex rounded heavily built temporal crest. The right temporal crest, which has a rough surface for muscle attachment, is heavier built than on the left side which is smooth. The temporal crests are not overhanging the temporal fossa, at least not posteriorly. Instead, the angle between fronto-parietal and temporal planes (as far as preserved) is obtuse. The minimum transverse distance between the temporal crest (measurement D3) amounts to 50e mm. A bony ridge separates the lachrymal depression from the adjacent frontal

A third skull fragment preserving the fronto-parietal region is specimen GSI No LR-3597, excavated at Lonrong. This is the only specimen in which the parietales are preserved and it has part of the superior part of the occipital as well. On the left side a small posterior part of the orbit remains. The surface of the parietal is partly damaged

in the middle, but the outline in superior view is complete. Like the previous specimens, a sagittal crest is also well developed over the entire length of the frontals. This crest widens posteriorly and fades out before passing onto the parietals. The lateral margins of the fronto-parietal plane are bounded on both sides by well developed temporal crests, much sharper and less rounded than in the Marale specimen. The right temporal crest is medially bordered by an elongate groove, which is not developed on the left side. As with the Marale fragment, there is thus a strong asymmetry in the development of the temporal ridges.

Another feature that can be clearly observed in specimen GSI No LR-3597 is the angle between the frontal and parietal planes, the parietal plane bending down sharply relative to the frontal plane, resulting in a convex lateral profile. The minimum width between the temporal crest is 87 mm, showing that this was a larger individual than represented by the Marale skull fragment (**Table 8**). The distance between the sagittal crest and the left postorbital process (of which the tip is broken) measures 64+mm, showing that the maximum frontal width must have been slightly more than 128+ mm. The fronto-nasal suture is not preserved, but the total length of this skull fragment along the sagittal plane and as far as preserved from supra-occipital crest to the anterior broken edge of the frontal (which is approximately in the middle between the orbitals), is 138+ mm. In caudal view the upper portion of the occipital has a convex margin with a strongly developed and slightly overhanging supra-occipital crest (**Fig. 5-3**) that merges on both sides in the para-occipital crests.

On the left side, the occipital is preserved down to the transition with the processes temporalis, and the distance from the weakly developed median crest and the left margin of the occipital measures 63.5 mm. Thus the maximum width of the occipital

must have been close to $2 \times 63.5 = 127$ mm. On both sides of the median crest, the concave occipitals are laterally bordered by heavily developed tuberosities for attachment of the nuchal ligaments. The angle between frontal and occipital plane is approximately 97° , but can not be accurately measured because the superficial damage of the parietal in the middle.



Figure 5-3. Skull fragment of *Celebochoerus* from Lonrong (LR 3597).

Another specimen (GSI No LR3501), also from the Lonrong excavation, is more fragmentary than the previous one described above. Despite its fragmentary status, this frontal fragment clearly belonged to an even larger individual than the previous one. It is a median portion of the frontal area, including a very heavily built sagittal crest, and the temporal crest of the right side is partly preserved. The original

minimum width between both the temporal crests (measurement D3) can be estimated to have been around 116 mm, versus 87 mm for the previous specimen (**Table 8**).

The Mandible

The mandible of the Lakibong specimen (location GSI No 16/SCL/030/PG) consists of both horizontal rami and the symphysis. The right side contains the last premolar, a M₁ broken half along the lingual side, a slightly anteriorly damaged M₂ and the fully erupted, complete third molar. The left ramus just contains a complete P₄ and M₂ whereas the M₁ and the M₃ are broken. Both canines and all incisors are lost, but their alveoli are preserved.

At the diastema between the canine alveolus and the roots of the P₃ there are no additional roots or alveoli developed. Therefore, the first and second premolars must have been fully reduced at both sides, as in *Celebochoerus* mandible fragments described by Hooijer (1954, 1972). As in *Phacochoerus* and *Babyrousa* the anterior premolars were fully reduced, unlike *Sus*, where the P₁ and P₂ are still present and functional.

An aspect of mandible morphology of *Celebochoerus* that has not been noted previously is the U shaped symphysis in dorsal aspect. In contrast, *Sus* has a symphysis that are V shaped (**Fig. 5.4**). Another *Celebochoerus* mandible from the excavation site Lakibong 2 (GSI No. 1850) has one tooth, the left incisor I₂ in place. The tooth is spatulate distally, but narrow and becomes wedge shaped towards the neck. The other incisors are lost, but judging from the larger size of the alveoli it can be seen that the I₂ was smaller than the missing I₃.



Figure 5-4. *Celebochoerus* lower jaw (GSI No 16/SCL/030/PG) left occlusal view, and Lak.2 No.1850 (right ventral view) surface collected at Lakibong and compared with *Sus scrofa* mandible.

Lower premolars

The Lakibong mandible specimen no 16/SCL/030/PG lacks alveoli for P_1 and P_2 , but the P_3 was originally present as can be deduced from its alveoli. The P_4 is preserved and has a single triangular cusp with a flat labial and lingual surface. This premolar is worn, at the posterior side more so than anteriorly. The crown thus has a trapezoidal outline and has a well developed posterior ridge and cusp, which is less than half the height of the main cusp.

Based on measurement of lower teeth in *Celebochoerus* (**Table 5**), it follows that the P_4 is about the same width as the M_1 and narrower than the M_2 .

Molars

As already shown by Hooijer (1954), the molars of this fossil species have a much simpler structure as those of *Sus*, which has deep radial folds in the anterior, median and posterior surfaces of the main cusps. The simple molar structure of *Celebochoerus* is also seen in *Potamochoerus* and *Babyroussa*, as well as in many of

the primitive fossil suids. These specimens are all consistent with the general evolution stage of suids in the Miocene and Pliocene.

The lower canines

Concerning the morphology of lower canines from the Sengkang Basin fossil assemblages, in all specimens examined the posterior surface is narrower than the external surface. This characteristic also referred to as “verrucosic” type lower canines, a distinctive used by Pilgrim (1926) and subsequent workers in suid taxonomy to distinguish the warty pigs of the genus *Sus* (e.g. *Sus verrucosus*) from the non-warty pigs such as *Sus scrofa*.

The latter are referred to as having a “scrofie” type of lower canine in which the posterior surface of the lower canine is broader than the exterior surface. Hooijer (1954) described various lower canine fragments, but had no complete lower canines at his disposal. However, in the collections from the Lonrong and Lakibong excavations, there are several complete lower canines. Specimen GRDC No LR3603 (dextral) from Lonrong is covered with enamel on two sides, but not on the posterior surface (the surface that is in contact with the upper canines) (See Fig. 5-5). The maximum length of this specimen is 119+ mm measured along the ventral convex curvature of the tooth.

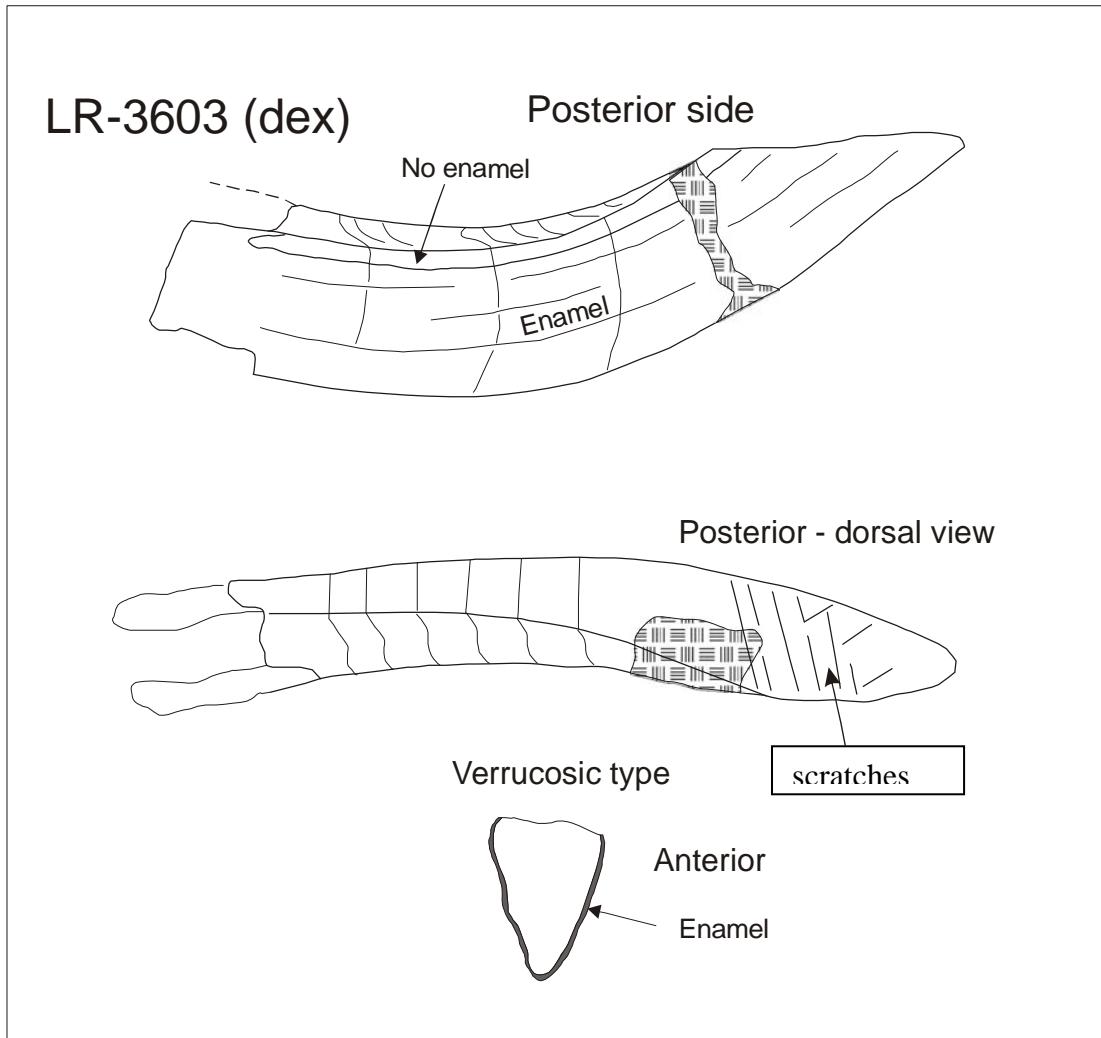


Figure 5-5 The *Celebochoerus* lower canines from Lonrong excavation (GRDC No. LR3603 dextral).

The Upper canines

Concerning *Celebochoerus* upper canines, the measured antero-posterior widths vary between 36.6-48.1 mm and the transverse widths between 30.4 and 40.1 mm, while lengths of complete examples are 177.1 to 217.9 mm straight and 242.9 to 294.4 along the outer curvature (**Fig.5-6; Table 6**). These ranges include a specimen described by Hooijer (1948, 1954; see table 3) and specimen collected subsequently.

On this basis, lower canines are not only narrower than uppers, but they are also decidedly shorter. The upper canines show related concave wear-facets on the proximal half of the anterior surface; again *Celebochoerus* canines are similar to those of African warthogs, and differ from those of *Sus* and *Potamochoerus*, in which the lower and upper canines meet each other at a sharper angle and no part of the upper canines project beyond the lower ones.

Figure. 5-6a. *Celebochoerus* upper canine in lingual profile



Fig. 5-6b. *Celebochoerus* upper canine from Lonrong in labial profile (LR 2524)



Table3. *Celebochoerus* upper canine measurements by Hooijer 1972, corrected by statistic formula

No Upper Canines	DAP/DT	Male (mm)	Female (mm)	Range	Mean (M_d)
1	DAP	43	-	DAP= 37-44	DAP= 39.875
	DT	39			
	DAP	44	-		
	DT	38			
	DAP	38	-		
	DT	31			
	DAP	40	-		
	DT	36			
	DAP	37	-		
	DT	31			
6	DAP	38	-	DT= 31-39	DT= 34.375
	DT	32			
	DAP	37	-		
	DT	32			
	DAP	42	-		
	DT	36			
	DAP	-	25		
	DT		23		
	DAP	-	24		
	DT		22		
11	DAP	-	25	DAP= 24-28	DAP= 25.286
	DT		21		
	DAP	-	25		
	DT		24		
	DAP	-	28		
	DT		26		
	DAP	-	25		
	DT		26		
	DAP	-	25		
	DT		22		
15	DAP	-	25	DT= 21-26	DT= 23.428
	DT		22		

Table 4. *Celebochoerus heekereni* upper teeth measurements (mm)

No. location/ specimen	P ⁴	M ¹	M ²	M ³	Range
LR 3625 (DAP) (DT)	15.4	14.2	15.9	21.3	
	11.5	16	16.1	19	
LR 2715 (DAP) (DT)	-	-	18.1	27.6	
	-	-	16.6	18.1	
LR 3624 (DAP) (DT)	-	-	-	29.3	
	-	-	-	18.6	
TA 0722 (DAP) (DT)	-	-	-	30	
	-	-	-	16.3	

Table 5. *Celebochoerus heekereni* lower molar/premolar measurements (mm)

No location/ specimen	P ₃	P ₄	M ₁	M ₂	M ₃	Range
BC 2973 (DAP) (DT)	13.6	14.7	16	18.6	lost	
	8.1	10.1	11.7	13.9	lost	
TA 07-5 (DAP) (DT)	-	broken	16.6	18.7	25.8	
	-	broken	12.8	13.8	14.4	
LR 2535 (DAP) (DT)	-	-	lost	22.9	30.4	
	-	-	lost	16.5	16.6	
LR 2716 (DAP) (DT)	-	-	lost	lost	30.7	
	-	-	lost	lost	17.4	
TA 07-4 (DAP) (DT)	-	-	lost	lost	28.3	
	-	-	lost	lost	14.4	
L2-1850 (DAP) (DT)	-	lost	lost	broken	23	
	-	lost	lost	broken	14.8	

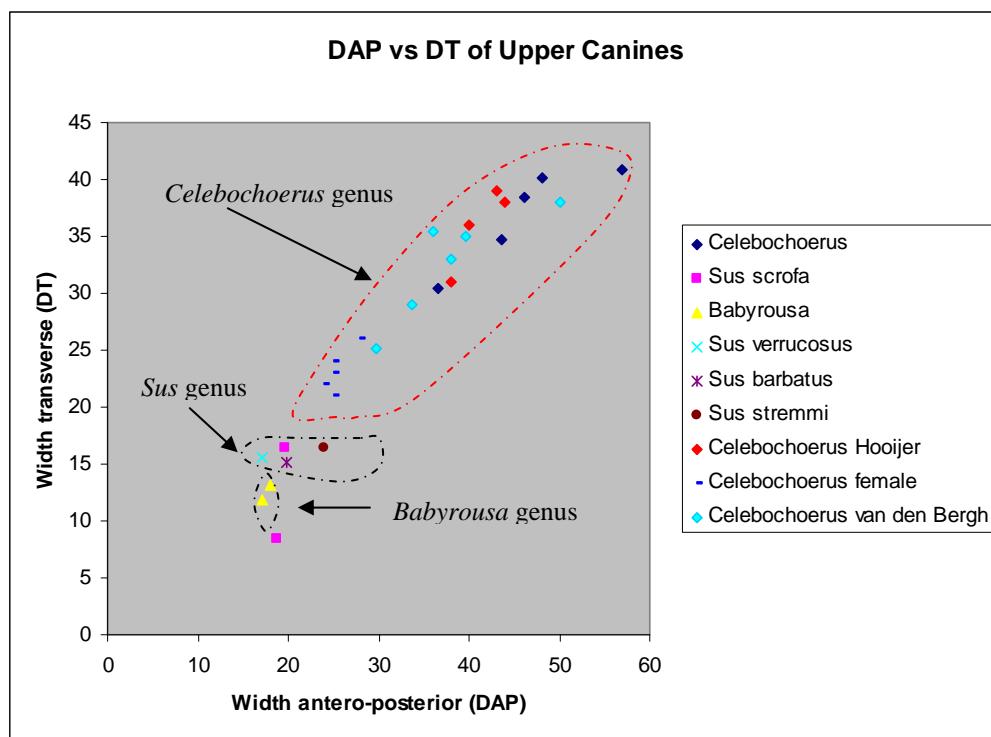
Table 6. *Celebochoerus*, upper canines measurements (mm), statistically corrected

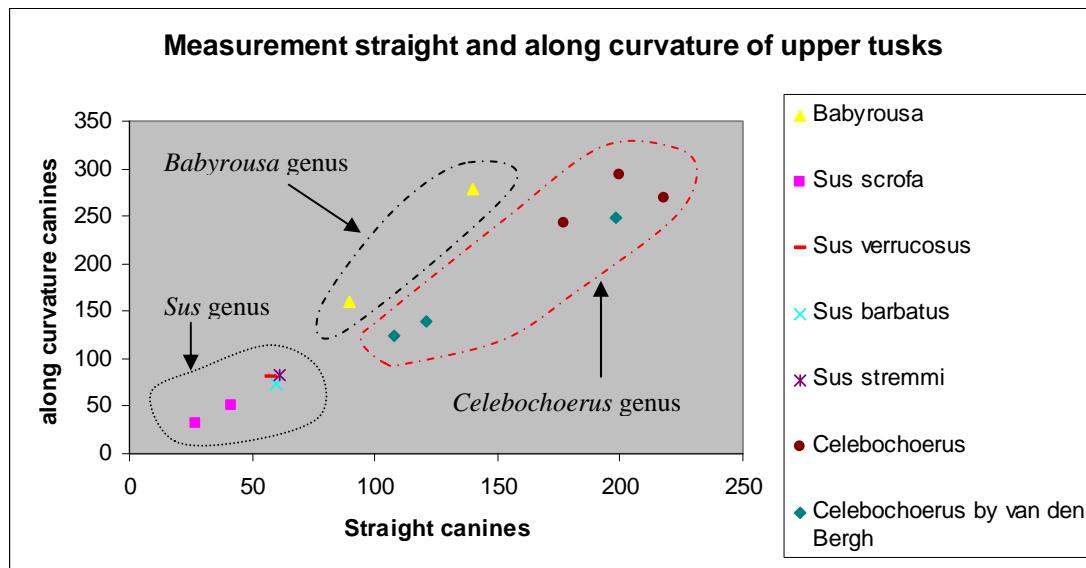
No Location	DAP	DT	H. canine straight	H. Canine along Curvature	Range	Mean (M _d)
LR 2534A	43.6	34.7	217.9	269.8	DAP= 36.6-48.1 DT= 30.4- 40.1	DAP = 43.625 DT = 35.925
LR 2704	36.6	30.4	reduced	reduced		
LR 2524	48.1	40.1	177.1	242.9		
JCLS.890622-2	46.2	38.5	199.7	294.4		

V.3. Comparison with *Babyroussa* and other extant and extinct Suidae

To investigate possible phylogenetic relationships between *Celebochoerus* and other genera of recent and fossil suids, including *Babyroussa*, I undertook comparative analyses of their measured cranial and mandibular traits, using specimens held in the collections of the Museum Zoology Bogoriense at Bogor and the Geology Museum at Bandung. The raw data used for my analyses is given in **Appendix 2**, while statistical comparison between the data for *Celebochoerus*, *Babyroussa* and *Sus* is summarized in **Figs. 5-7 to 5-9**.

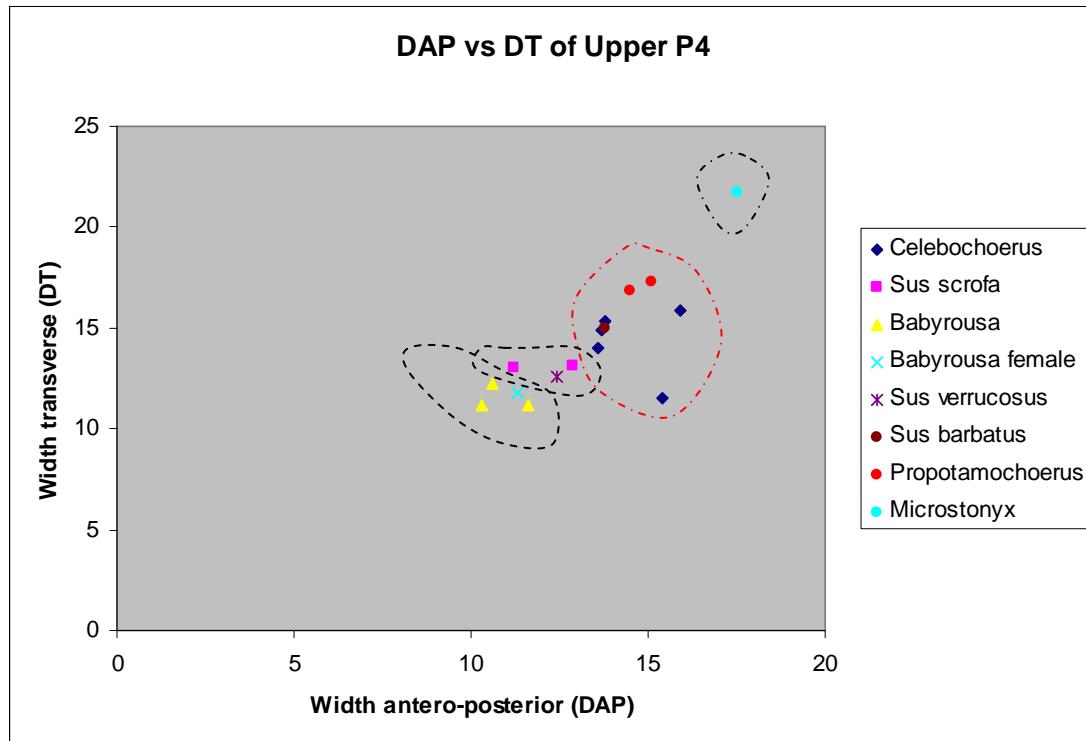
Figure 5-7. Metrical comparison of upper canine teeth from *Celebochoerus* and other suid genera
a. DAP vs. DT; b. straight vs. curved measurements

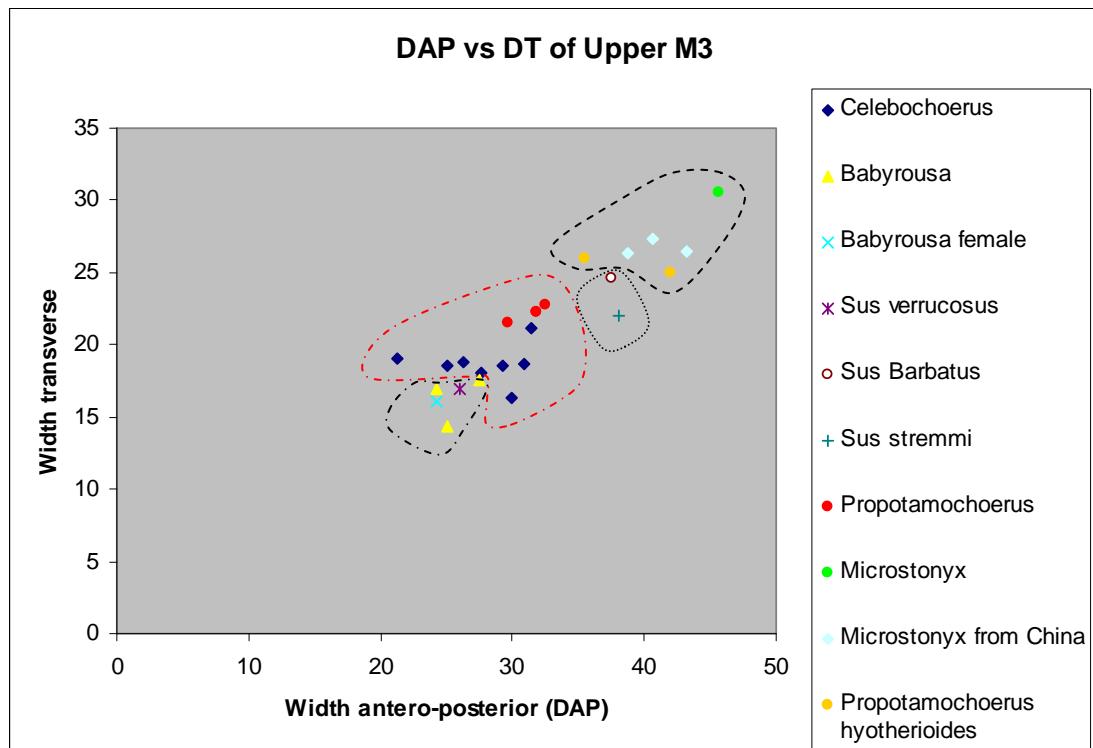




B. straight vs. along curvature of upper canines

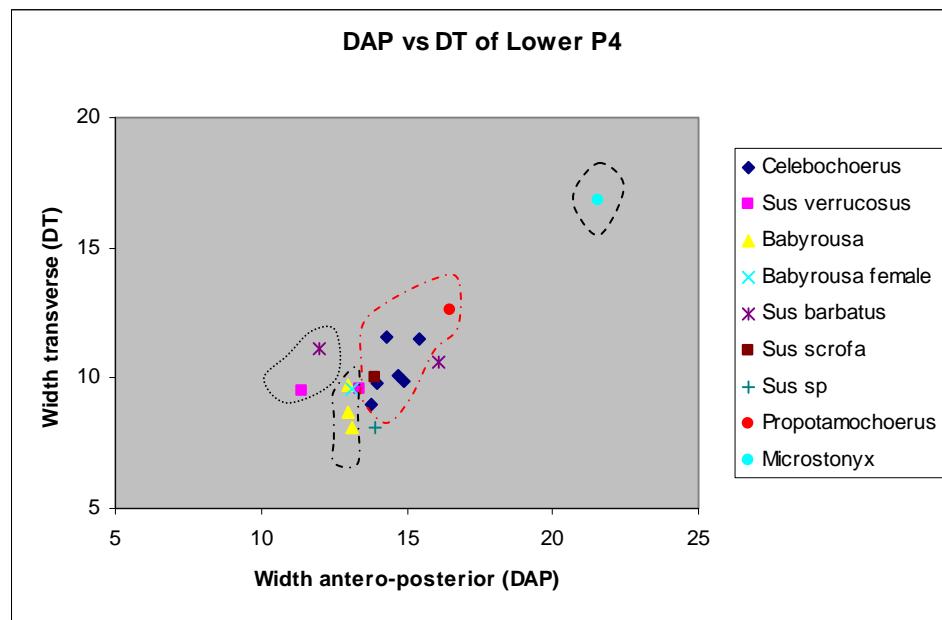
Figure.5-8. Metrical comparison of upper dentition from *Celebochoerus* and other suid genera
a. Upper last premolar; b. Upper third molar

a. Metrical comparison of upper last premolars from *Celebochoerus* and other suid genera.

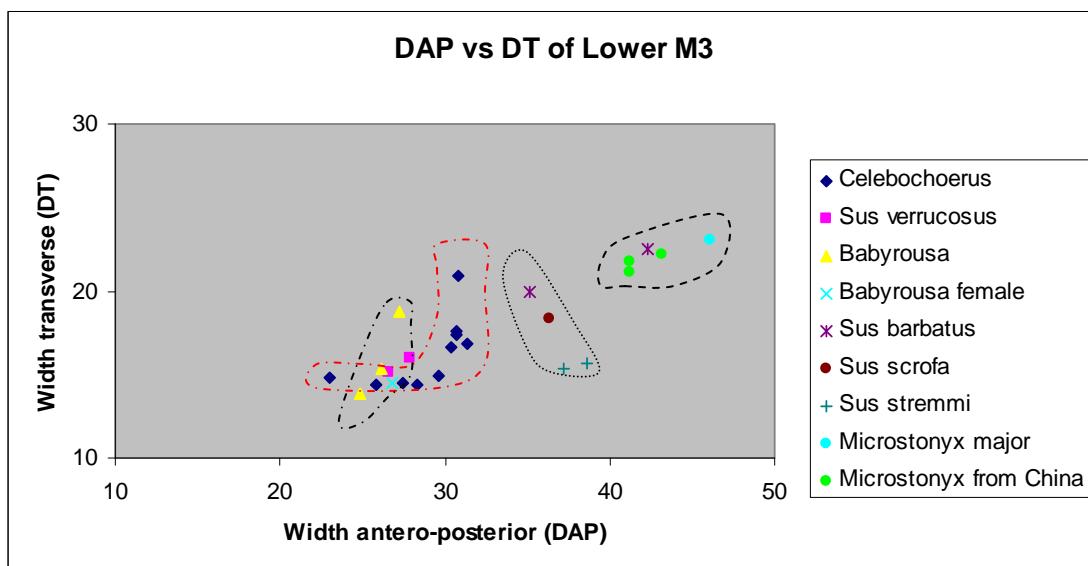


b. Upper third molars

Figure 5-9. Comparison of upper dentition between *Celebochoerus* and other extinct and extant genera
a. Lower last premolar; b. Lower third molar



a. Lower last premolars



a. Lower third molars

V.4. Conclusion

Comparative analyses of both qualitative and quantitative morphological traits clearly shows that *Celebochoerus* is morphologically distinct from *Sus* - as seen in the sagittal crest on the wide fronto-parietal area, the large size of the upper canines and the reduction of the number of enamel bands developed on the upper canines, the reduction of P₁ and P₂, the relative large size of the intermediate molars, the relative small size of the M³s, the reduction of the infraorbital fossa for the *levator rostri muscles*, and the transversely projecting zygomatic arches.

Suid evolutionary developments and divergences that occurred in the Miocene Period are therefore of particular interest in reconstructing the phylogenetic history of the *Celebochoerus* lineage – including when the ancestral population first reached Sulawesi, the length of time it was isolated prior to the time from which we have the first fossil evidence; and when the lineage became extinct. These issues, in the context of regional tectonic and climatic events, will be taken up in Chapter Six.

CHAPTER SIX

DISCUSSION AND CONCLUSION

VI.1. Introduction

The Chapter Five described some of the metrical and non-metrical anatomical traits of *Celebochoerus* and compared these with those of other recent and extinct Suids. Such evidence can be used to infer the phylogenetic position of *Celebochoerus* on the Suidae family tree, and thereby when the ancestral taxon crossed from Sundaland to Sulawesi, and how.

Representatives of three suid genera are known to have lived on Sulawesi – *Celebochoerus heeckereni* evident in the fossil record from Pliocene to Middle Pleistocene times; the extant *Sus celebensis* from Middle Pleistocene times; and the extant *Babyrousa babyrussa*, from Late Pleistocene times. Evidence for the phylogeny of these three relevant genera are summarised below.

VI.2. Phylogeny of the genus *Celebochoerus*

Previous researchers observed that *Celebochoerus heeckereni*, was not closely related to extant Sulawesi suids, but a number of morphological characteristics of the species provide clues as to when and where the ancestors may have originated (Hooijer, 1954, 1972; Aziz, 1990 and van den Bergh, 1999). These include:

1. Primitive, simple type of molars with thick and very weakly folded enamel lacking the development of extra lobes, distinct cusps. The talon in M^3 and talonid in M_3 are small.

2. Two premolars in the mandible, three in the maxilla (reduction of the anterior premolars is likely linked to the next characteristic: large size of upper canines).
3. Large, sideways projecting upper canines that may or may not possess a single enamel band at the anterior edge below. Upper canines originating from heavy built tubular alveoli lacking a bony ridge (jugum caninum) at the upper surface.
4. Cross-sectional shape of the lower canines as in *Sus verrucosus*. Enamel covers both the external and internal surfaces of the canines.
5. Strong development of the facial crest with the zygomatic process of the maxillary projecting sideways at a right angle to the longitudinal axis of the skull, as in *Potamochoerus*, not pointing backward and streamlined as in *Sus* or *Babyroussa*. Onset of facial crest is above the anterior part of M^3 , placed more forward than in *Sus* or *Potamochoerus*, but similar to *Propotamochoerus*.

A number of other traits can now be added to this list on the basis of the fossil traits described in Chapter Five. These are:

6. U-shaped mandibular symphysis, similar to that of primitive Suidae taxa (i.e. *Microstonyx*, *Paleochoerus*, *Hyotherium*).
7. Comparatively wide fronto-parietal area of the skull.
8. A strong sagittal crest developed on the fronto-parietal plane.
9. Occipital area wider than in *Sus* and *Babyroussa*.

-
10. Lachrymal arch weakly developed, lachrymal-maxilla-zygomatic junction flat or slightly convex, and lacking concavity (pre-orbital fossa), as developed in *Sus* and to a lesser extent in *Babyroussa*.

POINT 1

The morphology of *Celebochoerus heekereni* molars is comparatively simple, as in *Babyroussa*, and lacks the complexity evident in molars of *Sus*, which have deep radial folds and many accessory conules. The talon in M^3 and talonid in M_3 in *Celebochoerus* are also small (Hooijer, 1954); closely resembling those of *Paleochoerus* and *Propalaeochoerus* (see **Table 7** in **Appendix 3**). This fits with the general stage of suid molar evolution seen in many Miocene or Pliocene types.

POINT 2

Celebochoerus heekereni, has primitive premolar characteristics. For instance, the P_4 , is similar in shape to that of *Propotamochoerus*. Among the living genera of Suidae only *Potamochoerus* and *Babyroussa* also have lower premolars of this type. As noted by Hooijer (1954), the first and second premolars are also reduced, as they are in *Babyroussa* and *Phacochoerus*. This is not the case in other modern and extinct suid genera that have smaller upper canines. In addition, the primitive morphology of the remaining premolars is very similar to those of *Paleochoerus* from the Lower and Middle Miocene of the Siwaliks. Some of the advanced dental characteristics, most notably the enlargement of the upper canines and the associated reduction of the anterior premolars, are also shared with the African warthogs, but these may be attributed to parallel and independent evolution, possibly as an adaptation to more

open environments or savannah. In *Potamochoerus* and *Propaleochoerus* only the P₁ is reduced.

POINT 3

The wear facet on the anterior surface of the lower canines commences 5 cm from the base and then extends to the distal tip. However, the wear facet on the upper canines does not extend to the tip, indicating that they extended out beyond the lower canines. In addition, a single enamel band of variable width (0-15 mm) may be found on the anterior edge of the lower surface. In contrast, member species of genus *Sus* (extant and extinct) have more than one enamel band, on the inner and outer surface of the upper tusks. *Celebochoerus* also lacks a bony ridge or superior *jugum caninum* on the canine flanges as found in *Sus* and *Babyroussa*.

POINT 4

In *Celebochoerus heekereni* the flat posterior surface of the lower canines is narrower than the flat external surface, while the internal surface being wider than either of these. The same canine morphology is found in *Sus verrucosus*, and it is customary to refer to this as the *verrucosic* type, as compared with the *scrofa* canine type, in which the posterior surface is wider than the external one. Generally speaking, the *verrucosic* type of lower canine represents the primitive stage. Early members of the genus *Sus* (e.g. *Sus stremmi*) still have a *verrucosic* type of lower canine, whereas more advanced members possess a *scrofic* type. The Upper Miocene genera *Propotamochoerus* from the Siwaliks in South Asia and the recent *Potamochoerus* from Africa have a lower canine cross-section that lies midway between the *verrucosic* and *scrofic* types.

POINT 5

The onset of the zygomatic process of the *Celebochoerus heekereni* maxilla occurs abruptly, as seen in *Potamochoerus* and the Miocene *Propotamochoerus*, but unlike the more streamlined profile seen in *Sus*. In dorsal view, the anterior margin of the zygomatic arch, or facial crest, forms an angle with the sagittal plane around 100° - 110° in *Celebochoerus* (110° in *Potamochoerus*; ca. 90° in *Propotamochoerus*; ca. 90° in *Hyotherium*). Actually, the facial crest extends laterally from the longitudinal skull profile nearly perpendicular, whereas the facial crest in *Sus* points more backward with an angle of between 135° - 140° . In these skull features *Celebochoerus* (see Fig. 6-1) resembles the extinct primitive *Hyotherium dartevellai* from the Lower Miocene of East Africa, whereas *Microstonyx* from the Middle to Late Miocene of Eurasia has a more streamlined profile.

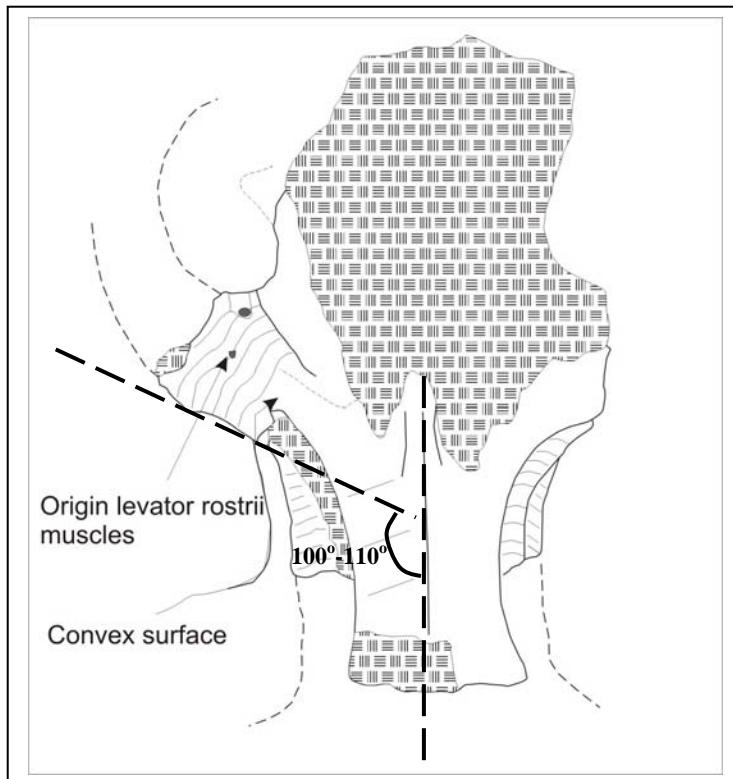


Figure 6-1 The zygomatic process of this *Celebochoerus* maxillary (GSI No. ABTL-161186-1B) projects sideways almost at right angles to the longitudinal axis of the skull.

POINT 6

In dorsal view the posterior border of the mandibular symphysis of *Celebochoerus* is U-shaped, similar to those found in Lower to Late Miocene pigs, such as *Microstonyx erymanthius* (Pilgrim 1926), *Microstonyx major* in China and Europe (Kostopoulos *et al.*, 2001), *Hyotherium dartevellai* in Africa (Wilkinson 1976) and *Propotamochoerus* sp. in the Balkans (Geraads *et al.*, 2008). This is very distinct from the V-shaped pattern found in *Sus* and *Babyrousa* (**Fig. 6-2**).

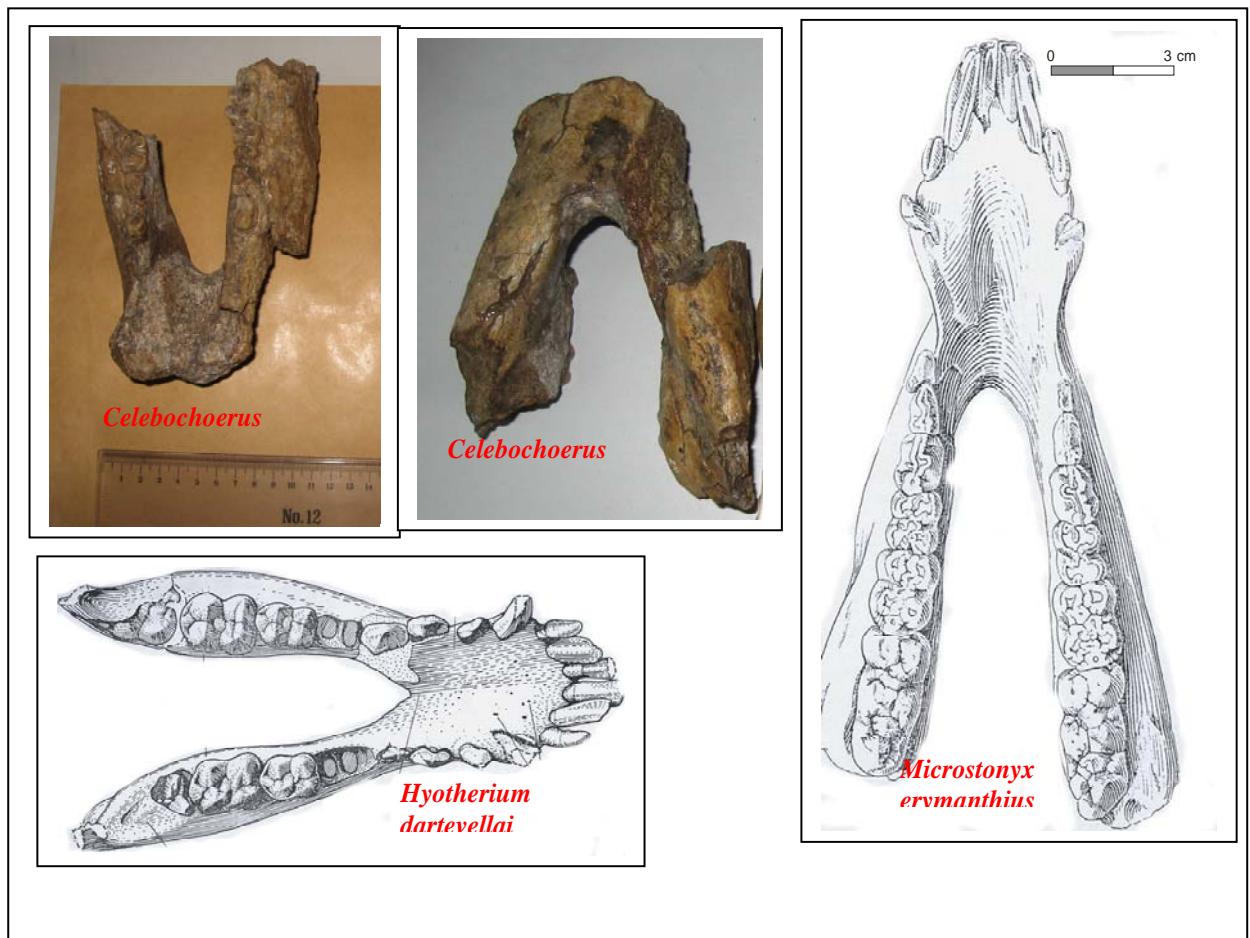


Figure 6-2 *Celebochoerus* lower jaw shape compared with that of *Microstonyx erymanthius* and *Hyotherium dartevellai*.

POINT 7

The minimum width of the parietal plane between the temporal fossa (measurement D3; **Fig. 2-3**) is much larger in *Celebochoerus* than in *Sus* or *Babyrousa*, with measurements ranging from 78 to 116 mm. In *Sus* measurement D3 varies between 8 and 40 mm and in *Babyrousa* between 12 and 29 mm. Though no measurements could be taken on skulls of the recent African *Hylochoerus meinertzhageni*, this species also has a relatively wide parietal region (**Fig. 4-5**). *Celebochoerus* however, has a flat inter-orbital region with a well-developed sagittal crest, whereas the inter-orbital region in *H. meinertzhageni* and its extinct progenitor *Kolpochoerus* is strongly concave.

POINT 8

Celebochoerus has a well-developed sagittal crest over the frontals and pariетals, as found in the Early Miocene *Hyotherium dartevellai* from East Africa (**Fig. 5-2**). Such a crest does not occur in *Sus*, *Babyrousa* or other extant genera (e.g. *Phacochoerus*, *Hylochoerus*, *Potamochoerus*). Nor is it found in *Propotamochoerus* and *Microstonyx*, which have flattened frontoparietal regions.

POINT 9

Celebochoerus has a wider and less concave occipital surface than that of *Sus* and *Babyroussa*. (See occipital fragment GSI No LR3597; **Fig. 5-3**; and **Appendix 2**).

POINT 10

In lateral profile, the lachrymal or pre-orbital fossa, which is the attachment for the *elevator rostrii* muscles, is almost convex in *Celebochoerus*, but concave in *Sus*, *Babyrousa* and most other Miocene and Pliocene suid genera. This distinctive character in *Celebochoerus* most resembles that of *Paleochoerus* known from the Siwaliks.

Concerning *Celebochoerus* phylogeny, the skull and dental morphologic traits for *Celebochoerus*, recent suids, and a selection of fossil suidae of which cranial material are summarised in **Table 7, Appendix 3**. Amongst these taxa, *Celebochoerus* is quite unique in having a well-developed sagittal crest on the dorsal surface of the braincase, a characteristic also developed in *Hyotherium dartevellai*, but not encountered in any of the other suids studied. A relatively wide parietal surface between the temporal fossa and the presence of strongly built temporal crest is shared only with the recent *Hylochoerus* and its direct ancestor *Kolpochoerus*, and in the ancestor of the recent *Phacochoerus*, the extinct *Metridiochoerus*. However, in the latter lineages, there is no sagittal crest on the dorsal surface of the braincase. In contrast, the interorbital area is strongly concave.

Another characteristic feature of *Celebochoerus* is the broad, heavily built zygomatic arch that projects sideward. In this character, it resembles the extant *Hylochoerus* lineage, but also the extinct genera, *Metridiochoerus*, *Microstonyx*, *Kolpochoerus* and *Hyotherium*. The most parsimonious explanation would be that *Celebochoerus* was derived from a common ancestor with *Kolpochoerus*, *Metridiochoerus*, and *Microstonyx*. Generally, *Paleochoerus* is considered as the common ancestor of all these lineages. Because *Paleochoerus* is mostly known from its dentition, and known

skull material is very fragmentary, it was not possible to compare all skull characteristics present in *Celebochoerus* with those in *Paleochoerus*. For instance, we do not know the shape of the fronto-parietal region in the latter. With the available evidence, *Paleochoerus* seems to be the most likely ancestral candidate for *Celebochoerus*.

Paleochoerus is known from the Early to Middle Miocene of the Siwaliks. Therefore, the ancestor of *Celebochoerus* probably arrived on South Sulawesi during the Miocene. There were almost certainly never any continuous ‘land-bridge’ between Sulawesi and the Asian mainland at least since the Miocene, but probably since the Middle Eocene (see Chapter Three). Therefore, the ancestral form must have crossed a sea barrier to reach South Sulawesi. This could have been during the Middle Miocene, when deltaic environments extended much further into the Makassar Straits and the required sea crossing would have been smaller than today.

VI.3. Phylogeny of the genus *Sus* in Java and Sulawesi

The oldest evidence for subfamily Suinae in Indonesia is the extinct *Sus stremmi* Koenigswald 1933 that lived in Java. Identification of this poorly known species was initially based on a mandible from the Upper Kaliglagah Series in the Bumiayu area of western Central Java, dated between 1 and 2 Ma (Aziz, 1990). Subsequently, fossils of *Sus stremmi* were also found in the Black Clays (Sangiran Formation) of the Sangiran area in East Java dating back to 1.6 Ma.

Sus stremmi is probably directly ancestral to *S. verrucosus*, *S. terhaari*, *S. barbatus* and *S. brachygynathus* (Dubois vide Hardjasasmita, 1987). On the basis of similarities in molar and canine morphology, the last-named species probably gave rise to the

Middle Pleistocene *S. macrognathus* (Aziz 1990). In fact, the main difference between these two *Sus* species is in size of cranium and teeth, which are probably due to different paleoenvironmental conditions, since many other taxa also show size reduction over the same time period (van den Bergh 1999).

While *S. stremmi* is considered ancestral to all other modern warty *Sus* species in the Indonesian Archipelago, its advanced molar morphology, means that it (or any other Pliocene or Pleistocene suid from Java) could not have given rise to *Celebochoerus*, which was present on Sulawesi from at least 2.5 Ma and possibly much earlier (van den Bergh, 1999). At the time, most of Java was still below sea level and has yielded no suid remains of this age.

Sus stremmi is clearly from a different lineage than *Celebochoerus*. For instance, in cross-sectional profile the upper canines of *S. stremmi* are thinner than *Celebochoerus*; the lower canines are of *verrucosic* type; and in common with all other fossil and extant *Sus* species, the upper tusks of *Sus stremmi* possess two or more enamel bands, whereas *Celebochoerus* has a single band ventrally or none at all. This suggests that the enamel is in the process of reduction in *Celebochoerus*.

However, *S. stremmi* still sheds some light on the ancestry of the extant *Sus celebensis*. Dental elements attributed to *Sus celebensis*, one of the two extant pigs of Sulawesi, are known from Holocene sites in South Sulawesi (Hooijer, 1950) and from a single skull fragment from the Paciro River, also in South Sulawesi (Hooijer, 1969). Though the exact provenance of this skull is not known, van den Bergh (1999) has suggested that it likely originates from the Tanrung Formation, with an estimated Middle Pleistocene age. In addition, mtDNA studies suggest that *S. celebensis* may

have split off from the other Indonesian *Sus* lineages around the Middle to Late Pleistocene (Funk et al, 2007 and Hardjasasmita, 1987).

In skull and molar morphology, *S. celebensis* is similar to the *verrucosus* group. It is therefore believed that the ancestor of *Sus celebensis* migrated from Sundaland to Sulawesi by crossing the Makassar Strait from eastern Borneo during the Lower or Middle Pleistocene. At this time in Java had just two successive suid species - i.e. *Sus bracygnathus* around 900 ka, followed by its descendant species *Sus macrognathus* between ~800 and 150 ka. *Sus macrognathus* may have crossed to Sulawesi somewhere during this interval and evolved into *S. celebensis*.

Possibly the extinction of *Celebochoerus* in Sulawesi and some *Sus* species in Java during the Pleistocene transition may have been caused by interspecific competition, or to increasing climatic instability. More specifically, it is possible that the arrival of *Sus celebensis* in Sulawesi caused a *Celebochoerus* population decline and even its extinction. Significantly, some *Sus* species (*Sus verrucosus* and *Sus barbatus*) are presently in decline after *Sus scrofa* entered Java.

VI.4. Phylogeny of the genus *Babyroussa*

Comparative analyses of Suidae mtDNA consistently show that *Babirusa* is the most distant suid lineage relative to *Sus* and all other extant pig taxa (Funk et al 2007). In fact, a range of phylogenetic evidence indicates that *Babirusa* is the most primitive of living pig species, and that it has been genetically isolated on Sulawesi for a very long time - probably since the Middle Miocene. On the basis of its primitive molar and premolar morphology, most researchers believe that *Babirusa* is derived from an Early Miocene or even Oligocene ancestor (Thenius, 1970; Groves, 1981).

Babyroussa is the only species where the enamel bands have completely disappeared from the upper canines. Its molars, however, are very similar to those of *Celebochoerus*. It could therefore be argued that *Babyroussa* evolved from *Celebochoerus* by undergoing full reduction of the enamel band and size of the upper canines combined with their upward rotation. However, this is unlikely because the skull morphology of *Babirusa* has very distinctive traits, such as the lack of a sagittal crest, the narrow fronto-parietal plane, the narrow occipital plane, the backward projecting and lightly built zygomatic arch, the angulated muzzle and the well-developed infraorbital fossa for attachment of the *levator rostri* muscle. Instead *Celebochoerus* and *Babyroussa* are two primitives, but quite distinct genera on the suid family tree (see Fig. 6-3).

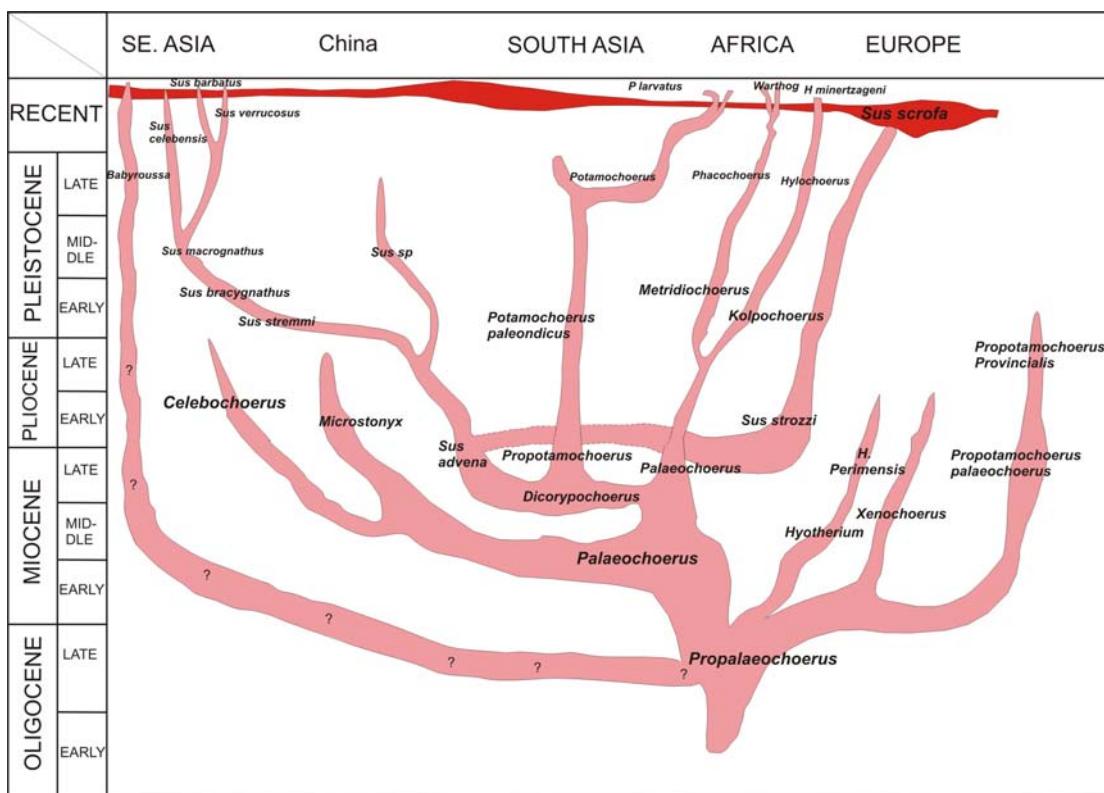


Figure 6-3 *Celebochoerus* lineage in the family tree of Suidae

VI.5. The palaeoenvironmental context

Early Miocene –Late Miocene

Pollen records from thick lacustrine and fluviatile sedimentary sequences from the Java Sea, the Malay Basin, the Natuna Sea and Sumatera, show that Southeast Asian landscapes of the time were dominated by subhumid or monsoonal vegetation. However, from 20 Ma onwards rainforests expanded across Sundaland, as far north as southern China (Morley, 1999, 2000).

Southwest Sulawesi was already exposed as dry land. This is evident in the widespread distribution of the Camba volcanic formation, which was deposited in the western part of the Walanae depression in the Early to Late Miocene; a time when the eastern part was predominantly shallow marine, with little land exposed.

In the Middle Miocene, perhumid climate vegetation (freshwater marsh and swamp communities) expanded across Java, Sumatera, and the Malay Peninsula, as evidenced by pollen assemblages in lacustrine shale and fluvial sandstone facies (Morley, 2000). This was followed, in the Middle to early Late Miocene (before 15 Ma), by a period of drier climates favouring open savannah woodland, which replaced rainforest, possibly during periods of low sea level (Moss and Wilson, 1998; Morley 2000 and Meijaard, 2003).

Early Pliocene to Early Pleistocene

In the Early to Middle Pliocene (ca. 4.5-3.5 Ma), there is evidence of much higher sea levels, ~100 m above present-day levels, and Borneo became separated from the

Asian mainland (Haq et al, 1987; Mc Neill et al, 1998). In East Borneo, the Mahakam River carried a large volume of sediment, which it mainly deposited in a delta, which prograded west throughout the Pliocene, as it does today.

In Java, pollen indicates a savannah or open-woodland at the time (Semah, 1984; Pouhapessy, 1990 and Morley 2000, p.198-201). It was also a time of major volcanic activity.

Celebochoerus had already crossed to Sulawesi by the Late Pliocene, as evident by fossil remains in the Beru Member of the Walanae Formation, which are estimated to be 2.5 Ma in age (van den Bergh, 1999). Pollen assemblages in sediment samples from the Lakibong River and Parenring Village fossil sites indicate that they were deposited in estuarine-mangrove environments (Samples BRC 27 and 28. See Appendix 4), while foraminifera, nanoplankton and marine molluscs in the Beru Members indicate nearby open marine, outer sublitoral, and upper bathyal environments.

Early Pleistocene to Recent

The Early Pleistocene to Middle Pleistocene period is characterised by fluctuations in climate and sea level - with the latter varying between 70 and 100 metres below present sea level. It is also the time where Java and Sumatra both started to take on their present shape, when both were connected to the Asian mainland (Meijaard, 2003).

The earliest evidence for mammals on Java, the Ci Saat fauna, is also of Early Pleistocene age, and includes the first evidence in the region for *Sus* - *Sus stremmi*,

which was ancestral to the Middle to Late Pleistocene species *S. macrognathus*. The latter in turn appears to have been directly ancestral to the Sulawesi suid *S. celebensis*, fossilised remains of which were found in deposits of presumed Middle Pleistocene age. Java, Sumatra and Borneo only became separated from the Asian mainland and from each other with postglacial rises in sea level over the past 10,000 years.

VI.5. CONCLUSIONS

In this chapter, I have presented evidence for the dispersal and evolution of *Celebochoerus* in South Sulawesi, as well as its position on the Suidae family tree. The evidence includes the results of my quantitative and qualitative analyses of *Celebochoerus* remains.

A range of cranial and dental features, described in Section VI.1, indicates that *Celebochoerus* was derived from *Palaeochoerus*, a primitive suid genus known from the Lower Miocene of the Siwaliks in the Indian subcontinent (**Table 7 in Appendix 3**). If so, *Celebochoerus* subsequently underwent a reduction of the anterior premolars and an increase in the size of the upper canines. It is not descended from the Upper Miocene *Propotamochoerus*, as proposed by Hooijer (1954).

Palaeochoerus also appears to have been ancestral to the Early Pliocene *Microstonyx* in China; and to African suid genera *Metridiochoerus* and *Kolpochoerus*, and hence to extant African warthogs.

The palaeo-geographic history of Sulawesi, outlined in Chapter Three, indicates that sea crossings were always required to reach this island. However, in the Early Miocene, when *Palaeochoerus*, the genus ancestral to both *Celebochoerus* in

Sulawesi and *Microstonyx* in China, occurred in Asia there were prograding deltaic fronts along the coasts of Borneo and Sulawesi (Moss *et. al.*, 1999 in Meijaard, 2003). These deltas significantly reduced the sea crossing required to reach southwest Sulawesi from the Borneo section of the East Asian mainland, particularly at times of very low sea level - and pigs are reasonably adept at swimming (Meijaard, 2003). Tectonic uplift ~6.6 Ma terminated this process of progradation.

On the basis of (palaeo) geography, another obvious route for terrestrial animals reaching Sulawesi from the Borneo section of the Asian mainland was from the north via the Sulu Archipelago, Mindanao and small stepping-stone islands, such as Sangihe. Significantly, even today pigs can be observed swimming between islands of the Sulu Archipelago – when local residents often take the opportunity to hunt the animals (Eusebio Dizon: National Museum of the Philippines: pers. comm).

Celebochoerus occupied parts of Sulawesi until at least the terminal Pliocene/Lower Pleistocene. It therefore overlapped significantly in time with *Babiroussa* that, on the basis of primitive molar and premolar morphology, seems derived from the earlier, Late Oligocene to Early Miocene genus *Propaleochoerus* (Thenius 1970; Groves 1981; Section VI.4), but is still extant on Sulawesi. Despite this chronological overlap, fossil remains of *Celebochoerus* and *Babiroussa* have never been found in the same deposits in Sulawesi. In addition, evidence for the latter genus is conspicuously absent from the Walanae Formation and only dates to the last ~35,000 years at archaeological sites such as Leang Burung 2 (Glover 1981).

One implication is that in the Miocene to at least the end of the Pliocene, these suid genera probably occupied different palaeo-islands that later combined to help form present-day Sulawesi. The present-day distribution of other faunal species (e.g.

tarsiers and macaques) has similar implications (Merker and Groves 2006). If so, then early representatives of these two suid lineages probably colonised different palaeo-islands that now constitute Sulawesi, at different times, and using different migration routes.

In contrast, fossil evidence for the last pig to colonise South Sulawesi, *Sus celebensis*, and *Babiroussa* occurs throughout the same archaeological deposits from 35,000 years ago up until the present. This *Sus* species probably evolved from *Sus macrognathus* found in Middle to Late Pleistocene deposits of Java, when that island had land connections with Borneo. The evidence indicates that multiple suid colonisations of Sulawesi occurred over an extended period and probably via a number of routes from the east Borneo section of the Asia mainland.

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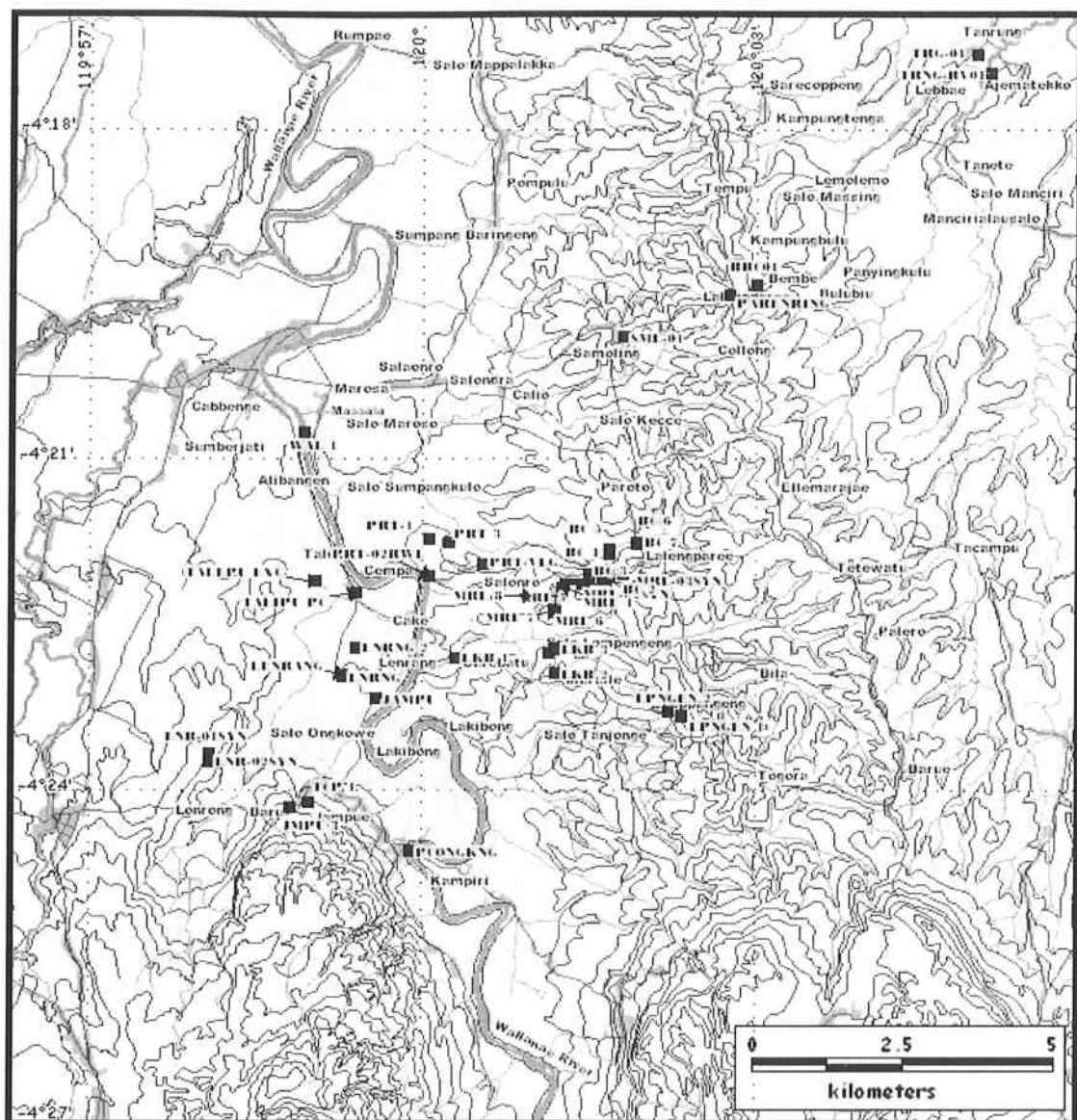
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Appendix 1



Map of the study area are showing samples location (Blue Square).

Appendix 2

Table 8. Dorsal and Occipital skull measurements

lower canine								
No	Coll nr	taxon	locality	dental wear age class	DAPc	DTc	H canine straight	H canine along curvature
1	C Grooves ANU	<i>Sus</i>	feral (Australia)	M1=c; M2=b; M3=a				
2	C Grooves ANU	<i>Sus</i>	domestic? -2 (Australia)	M1=d; M2=b; M3=a	12.4	8.9	22	23.9
3	GRDC	<i>Sus scrofa</i>	Java	M1=k; M2=f; M3=c	-			
4	GRDC	<i>Sus scrofa vittatus</i>	G.Lawu, Java	M1=f ; M2= d; M3= a				
5	MZB 15199	<i>Babyrousa babyrussa</i> (juvenile)	Sulawesi	M1= c; M2= b; M3= a	13.4	10.9	71.4	81.2
6	MZB 7046	<i>Babyrousa babyrussa</i>	Sulawesi	M1=g ; M2= e; M3= b	21.1	14.4	134.7	146.1
7	C Grooves ANU	<i>Babyrousa babyrussa</i>	?	M1=c; M2=b; M3=a	16.8	12.2	102.6	114.2
8	MZB 11953	<i>Sus celebensis</i> ?	Central Sulawesi	M1= j; M2= e; M3=c	20.4	11.2	59.8	60.5
9	MZB 22404	<i>Sus celebensis</i> ?	North Buton		20.1	13.6	62	65.4
10	MZB 15201	Female <i>B. babyrussa</i>	Sulawesi	M1=d ; M2=b ; M3= a	7.1	4.5	9.5	10
11	MZB 8367	<i>Sus barbatus</i>	Borneo	M1=k ; M2= j; M3=j	21	14.2	73.2	84.3
12	GRDC	<i>Sus barbatus</i>	Borneo	M1= ; M2= ; M3=	20.4	13	45.4	49.5
13	GRDC LR-3603	<i>Celebochoerus</i>	Sulawesi		25.2	16.5	128.3	135.2
14	Hooijer 1954	<i>Celebochoerus</i>	Sulawesi		24.3	15.5		
15	Hooijer 1954	<i>Celebochoerus</i>	Sulawesi		22.4	15.3		
16	Hooijer 1954	<i>Celebochoerus</i>	Sulawesi		22.5	14.5		
17	BC 2961 (van den Bergh)	<i>Celebochoerus</i>	Sulawesi		20.3	14.9		
18	LR 2650 (van den Bergh)	<i>Celebochoerus</i>	Sulawesi		23.7	17		
19	LK-2332	<i>Celebochoerus</i>	Sulawesi		28.2	18.2		

Lower Dentition (m2-m3)

No	Coll nr	TAXON	locality	dental wear age class	DAP m2	DT m2	wear stage m2	DAP m3	DT m3	wear stage m3
1	C Grooves ANU	<i>Sus</i>	feral (Australia)	M1=d; M2=b; M3=a	19.7	12.9	c	-	-	a
2	GRDC	<i>Sus scrofa</i>	Java	M1=k; M2=f; M3=c	20.8	15.5	j	36.3	18.3	c
3	GRDC	<i>Sus vittatus</i>	G.Lawu, Java	M1=f ; M2= d; M3= a						
4	MZB 15199	<i>Babyrousa babyrussa</i> (juvenile)	Sulawesi	M1= c; M2= b; M3= a	17.6	14.2	c	26.1	15.3	a
5	MZB 7046	<i>Babyrousa babyrussa</i>	Sulawesi	M1=g ; M2= e; M3= b	17.1	12.8	e	24.8	13.8	c
6	C Grooves ANU	<i>Babyrousa babyrussa</i>	?	M1=c; M2=b; M3=a	16.6	13	c	27.2	18.8	a
7	MZB 11953	<i>Sus verrucosus</i> ?	central Sulawesi	M1= j; M2= e; M3=c	17	14.4	f	27.9	16	d
8	MZB 22404	<i>Sus celebensis</i> ?	North Buton		17.6	13	g	26.6	15.1	d
9	MZB 15201	Female <i>B. babyrussa</i>	Sulawesi	M1=d ; M2=b ; M3= a	17.8	14.3	c	26.8	14.5	a
10	GRDC	<i>Sus barbatus</i>	Borneo	M1= ; M2= ; M3=	22.2	17	j	35.2	19.9	e
11	MZB 8367	<i>Sus Barbatus</i>	Borneo	M1=k ; M2= j; M3=j	22.7	19.2	k	42.3	22.5	j
12	GRDC SCL/030/Lak.16 No.47	<i>Celebochoerus</i>	Sulawesi		19.1	14.3	g	27.4	14.5	f
13	GRDC LR-2536	<i>Celebochoerus</i>	Sulawesi		23.5	19.1	g	30.8	20.9	d
14	Hooijer 1954	<i>Celebochoerus</i>	Sulawesi	M1=e ; M2= e; M3=c	21	15		31.4	16.8	
15	Hooijer 1954				19.7	13.9		29.6	14.9	
16	Hooijer 1954									
17	Hooijer 1954				19.8	16.3		30.7	17.6	
18	GRDC BC-2973	<i>Celebochoerus</i>	Sulawesi		18.6	13.9				
19	GRDC TA07-5	<i>Celebochoerus</i>	Sulawesi		18.7	13.8	j	25.8	14.4	e
20	GRDC LR-2535	<i>Celebochoerus</i>	Sulawesi		22.9	16.5	b	30.4	16.6	a
21	GRDC LR-2716	<i>Celebochoerus</i>	Sulawesi		lost			30.7	17.4	d
22	GRDC TA07-4	<i>Celebochoerus</i>	Sulawesi		lost			28.3	14.4	c
23	GRDC TA07-22	<i>Celebochoerus</i>	Sulawesi							
24	GRDC L.2.-1850	<i>Celebochoerus</i>	Sulawesi		Broken			23	14.8	a
25	GRDC K.635 (Koenigswald)	<i>Sus stremmi</i>	Ngandong		-			37.2	15.4	b
27	GRDC K.629	<i>Sus stremmi</i>	Ngandong		broken			38.6	15.7	c
28	MPV-L307 van der Made	<i>Propotamochoerus</i>	Bunol, Valencia		25.2	18.2				

	1998									
29	DGUV (FBB 215)					25.2	17.2			
30	DGUV (FB S4)					24.5	19			
31	NG 103 (van der Made, 1989)	<i>Microstonyx major</i>	Nagri, Siwaliks			29.1	20.5		46.1	23.1
32	Loc. 114 Pearson 1928	<i>Microstonyx erymanthius</i>	South China			25.3	20.2		41.2	21.8
	Loc. 114					27.5	17.9		41.2	21.1
	Loc. 114					27.6	19.8		43.2	22.2
33	Loc. 49 Pearson 1928	<i>Propotamochoerus</i>	Tan-Tsun China			24.4	15.6			

Lower premolars and first molar

No	Coll nr	taxon	locality	DAPp3	DTp3	DAP p4	DT p4	H p4	DAP m1	DT m1	wear stage
1	C Grooves ANU	<i>Sus</i>	domestic?-2 (Australia)	11.9	6.6	13.9	8.1	9.5+	16.5	10.2	d
2	GRDC	<i>Sus scrofa</i>	Java	12.6	7.1	13.9	10	8.4+	16.2	11.5	k
3	MZB 15199	<i>Babyrousa babyrussa</i> (juvenile)	Sulawesi	10.7	8.1	13	9.7	10.4+	14.4	11.2	e
4	MZB 7046	<i>Babyrousa babyrussa</i>	Sulawesi	13.7	6.8	13	8.7	10.6+	13.1	11.3	h
5	C Grooves ANU	<i>Babyrousa babyrussa</i>	?	10.1	5.4	13.1	8.1	9.2+	15.6	10.2	d
6	MZB 11953	<i>Sus verrucosus</i> ?	central Sulawesi	10.4	7.2	11.4	9.5	9.6	13	11.9	j
7	MZB 22404	<i>Sus celebensis</i> ?	North Buton	12.4	7.1	13.4	9.6	5+	14	10.4	k
8	MZB 15201	Female <i>B. babyrussa</i>	Sulawesi	11.3	7.5	13.1	9.6	8.9+	16.3	11	d
9	GRDC	<i>Sus barbatus</i>	Borneo	16.4	7.9	12	11.1	11.4+	17.6	13.2	L
10	MZB 8367	<i>Sus barbatus</i>	Borneo	15.1	6.6	16.1	10.6		17.6	14.4	m
11	GRDC SCL/030/Lak.16, No47	<i>Celebochoerus</i>	Sulawesi			13.8	9	5.4+	broken	broken	
12	GRDC BC2973	<i>Celebochoerus</i>	Bulu Cepo, Sulawesi	13.6	8.1	14.7	10.1	11.8	16	11.7	
13	GRDC TA07-5	<i>Celebochoerus</i>	Tanrung, Sulawesi						16.6	12.8	k
14	Hooijer (1954)	<i>Celebochoerus</i>	Sulawesi	14.3	10.6	15.4	11.5		15.7	13.2	
15		<i>Celebochoerus</i>	Sulawesi	15.7	8.9	14.3	11.6		16.4	11.6	
16		<i>Celebochoerus</i>	Sulawesi	12.8	7.3	14.9	9.9		17.4	11.5	
17		<i>Celebochoerus</i>	Sulawesi	13.3	7.7	14	9.8				
18	van der Made MPV (PAN 148)	<i>Propotamochoerus</i>	Bunol, Valencia			16.5	12.6				
19	van der made, 1989	<i>Microstonyx Major</i>	Nagri, Siwaliks			21.6	16.8		19.4	16.6	
20	NG 103		India (Pakistan)								
21	Pearson 1928	<i>Microstonyx erymanthius</i>	South China						20.9	15.3	
	Loc. 114								18.5	15.9	
	Loc. 114								19.3	14.3	
	Loc. 114								22.1	15.5	

UPPER CANINES MEASUREMENT							
No	Coll nr	taxon	locality	DAP C	DT C	H canine straight	H canine along curvature
1	C Grooves ANU	<i>Babyrousa babyrussa</i>	?	lost	lost	lost	
2	C Grooves ANU	<i>Sus</i>	feral (Australia)	16.8	12.1	41.5	45.5
3	C Grooves ANU	<i>Sus</i>	domestic?-2 (Australia)	13.9	10.4	27.7	36.2
4	GRDC	<i>Sus scrofa</i>	Java	19.6	16.5	41.7	51.2
6	GRDC	<i>Sus vittatus</i>	G.Lawu, Java	18.7	8.5	27.2	32.3
7	MZB 15199	<i>Babyrousa babyrussa</i> (juvenile)	Sulawesi	17.5	13.2	89.4	160.7
8	MZB 7046	<i>Babyrousa babyrussa</i>	Sulawesi	18	11.8	140.2	277.6
9	MZB 11953	<i>Sus verrucosus</i> ?	central Sulawesi	17.2	15.6	57.5	80.2
10	MZB 8367	<i>Sus Barbatus</i>	Borneo	19.9	15.2	60.1	73.6
11	GRDC LR-2534A	<i>Celebochoerus</i>	Lonrong, Sulawesi	43.6	34.7	217.9	269.8
12	GRDC LR-2704	<i>Celebochoerus</i>	Lonrong, Sulawesi	36.6	30.4		
13	GRDC ABTL-161186-IB lok 21	<i>Celebochoerus</i>	Sulawesi	56.9	40.8		
14	GRDC ABTL-161186-IA lok 21	<i>Celebochoerus</i>	Sulawesi				
15	GRDC LR-2524	<i>Celebochoerus</i>	Lonrong, Sulawesi	48.1	40.1	177.1	242.9
16	GRDC JCLS.890622-2	<i>Celebochoerus</i>	Sulawesi	46.2	38.5	199.7	294.4
17	GRDC K.624	<i>Sus stremmi</i>	Sangiran, Java				
18	GRDC K.634	<i>Sus stremmi</i>	Bumiayu, Java	23.9	16.4	61.3	82.6
19	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	43	39		
20	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	44	38		
21	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	38	31		
22	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	40	36		
23	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	25	23		

24	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	24	22		
25	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	25	21		
26	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	25	24		
27	Hooijer (1954)	<i>Celebochoerus</i>	Beru area? Sulawesi	28	26		
28	BC 2987 Sinistral	<i>Celebochoerus</i>	Bulu Cepo, Sulawesi	50.1	38		
29	LR 3657 Dextral	<i>Celebochoerus</i>	Lonrong, Sulawesi	29.8	25.2	108	124
30	LR 3602 Sinistral	<i>Celebochoerus</i>	Lonrong, Sulawesi	39.6	35	198.5	248
31	SB 2802 Dextral	<i>Celebochoerus</i>	Sare Batue, Sulawesi	36	35.5	121	140
32	S 3939 Sinistral	<i>Celebochoerus</i>	Sompe, Sulawesi	38.1	33		
33	TA 3710 Sinistral	<i>Celebochoerus</i>	Tanrung, Sulawesi	33.7	29		

Molars									
No	Coll nr	taxon	locality	DAP M2	DT M2	wear M2	DAP M3	DT M3	wear M3
1	C Grooves ANU	<i>Sus</i>	feral (Australia)	25.9	16.1	b	34.5	19.2	a
2	C Grooves ANU	<i>Sus</i>	domestic?-2 (Australia)	22.7	15.3	b	-	-	a
3	GRDC	<i>Sus scrofa</i>	Java	20.9	18.8	f	30.6	22.5	c
4	GRDC	<i>Sus barbatus</i>	Borneo						
5	GRDC	<i>Sus vittatus</i>	G.Lawu, Java	22	19.6	d	31.9	19.6	a
6	MZB 15199	<i>Babyrousa babyrussa (juvenile)</i>	Sulawesi	18.9	17	b	27.5	17.6	a
7	MZB 7046	<i>Babyrousa babyrussa</i>	Sulawesi	18.1	16.8	e	24.3	17	b
8	C Grooves ANU	<i>Babyrousa babyrussa</i>	?	17.8	14.6	b	25	14.3	a
9	MZB 11953	<i>Sus celebensis</i> ?	Central Sulawesi	18.6	17.5	e	26	16.9	c
10	MZB 22404	<i>Sus celebensis</i> ?	North Buton						
11	MZB 15201	Female <i>B. babyrussa</i>	Sulawesi	14.4	16.6	b	24.3	16.1	a
12	MZB 8367	<i>Sus barbatus</i>	Borneo	26.2	23.3	j	37.5	24.6	j
13	GRDC SCL/030/Lak.16, No 47	<i>Celebochoerus</i>	Lakibong, Sulawesi						
14	GRDC LR-2536	<i>Celebochoerus</i>	Lonrong, Sulawesi						
15	GRDC LR-3625	<i>Celebochoerus</i>	Lonrong, Sulawesi	15.9	16.1	e	21.3	19	c
16	GRDC LR-2715	<i>Celebochoerus</i>	Lonrong, Sulawesi	18.1	16.6	e	27.6	18.1	c
17	GRDC LR-3624	<i>Celebochoerus</i>	Lonrong, Sulawesi				29.3	18.6	b
18	Hooijer 1954	<i>Celebochoerus</i>	Beru area, Sulawesi	19.2	15.2		25.1	18.5	
19	Hooijer 1954	<i>Celebochoerus</i>	Beru area, Sulawesi	22.2	18.7		26.3	18.8	
20	Hooijer 1954	<i>Celebochoerus</i>	Beru area, Sulawesi	20.6	18.3		31.4	21.1	
21	Hooijer 1954	<i>Celebochoerus</i>	Beru area, Sulawesi	22.9	18.5		30.9	18.7	
22	Hooijer 1954	<i>Celebochoerus</i>	Beru area, Sulawesi	lost			30	16.3	f
23	GRDC K.624	<i>Sus stremmi</i>	Sangiran, Java	-			38.1	22	c
24	DGUv FB51 van der Made 1998	<i>Propotamochoerus</i>	Bunol, Valencia				31.8	22.3	
25	MPV (PAN 288)	<i>Propotamochoerus</i>					29.7	21.5	

26	MPV (BU S2)	<i>Propotamochoerus</i>					31.8	22.3	
27	MPV	<i>Propotamochoerus</i>					32.5	22.7	
28	B354 van der made, 1989	<i>Microstonyx Major</i>	Siwaliks India	29	25.2		45.6	30.5	
29	Loc. 114, Pearson 1928	<i>Microstonyx erymanthius</i>	South China	28.6	25.5		40.7	27.3	
	Loc. 114			27.3	24.4		43.2	26.5	
	Loc. 114			29.6	24.9		38.7	26.4	
30	Loc. 49, Pearson 1928	<i>Propotamochoerus hyotherioides</i>	Tan-Tsun China	24.5	21.6		35.5	26	
	Loc. 66			28.3	23.5		42	25	

16	GRDC	<i>Chelebochoerus</i> Hooijer (1954)	Celebes					15.9	15.9	16.4	15.2	
17	GRDC	Hooijer (1954)						13.6	14	19	15.1	
18	GRDC	Hooijer (1954)						13.8	15.3	15.5	14.5	
19	GRDC	Hooijer (1954)						13.7	14.9	17.6	14.6	
20	GRDC	Upper Canine										
	LR3624	<i>Sus stremmi</i>	Sangiran							-		
21	GRDC											
	BC2973	<i>Sus stremmi</i>	Bumiayu									
22	GRDC	Upper Canine										
	TA 07-5	<i>Sus stremmi</i>	Ngandong									
23	GRDC	Lower dextral teeth										
	LR 2534A	<i>Sus stremmi</i>	Ngandong									
24	van der Made 1998	<i>Propotamochoerus</i>	Bunol, Valencia					14.5	16.8			
	DGUU (FB 56)		Spain									
	DGUU (FBB 223)							15.1	17.3			
	DGUU (FB 55)									17.9	16.5	
25	van der made, 1989	<i>Microstonyx Major</i>	Siwaliks					17.5	21.7	23.5	21.1	
	B 354	<i>rigth maxilla</i>	India (Pakistan)									
26	Pearson 1928	<i>Microstonyx erymanthius</i>	South China							21.6	19.8	
	Loc. 114									20.3	19.4	
										21.9	19.1	

Appendix 3

Table.7. the characteristic of Tertiary fossil Suidae include Teeth, canines and skull from any literature

No	Genus	Premolar	Molar	Canines	Skull
1	<i>Microstonyx</i>	<ul style="list-style-type: none"> • P_1 and P_2 not reduced • P_3 – the main cusp is divided into three tubercles, internal talon is strong developed • P_4 protocone is well developed (paracone and metacane divided by shallow furrow). • Strong posterior cingulum 	<ul style="list-style-type: none"> • Mandible U shape • Strong development of talon in M^1/M^2 • Accessory cusps are more/less but low at first and second upper molars • M^3 – strong anterior cingulum 	<ul style="list-style-type: none"> • Small and Short, protrudes longitudinal • Scrofic type 	<ul style="list-style-type: none"> • Occipital wide and triangular • In lateral profile, the nasal appears to be slightly concave • The palate is elongate and relatively narrow • The zygomatic arches are strongly inflated and laterally extended • Their anterior end a planed above (M^1/M^2) • The maxillary foramen above the anterior of M^2 • Concave preorbital fossa
2	<i>Propotamochoerus</i>	<ul style="list-style-type: none"> • P_4 is large tooth midway size between M_1 and M_2. Its central cusp may be regarded as single. • P_1 and P_2 not reduced • P_4--- talon is well developed (has enamel surface) and show bicuspid character of the outer lobe and fairly open valley. 	<ul style="list-style-type: none"> • M^3 – has well marked talon 	<ul style="list-style-type: none"> • Lower canines is medium to large • Intermediate between scrofic and verrucosic type 	<ul style="list-style-type: none"> • Sagittal crest not developed • The jugal process of the maxillary springs out very suddenly from the surface of the cheek (it forms almost a right angle). • Width of the skull in the occipital region is relatively smaller than in <i>Paleochoerus</i> and <i>Potamochoerus</i>.

No	Genus	Premolar	Molar	Canines	Skull
3	<i>Dicoryphochoerus</i>	<ul style="list-style-type: none"> • P_2 not reduced • P_3 – well developed of internal talon and appears internal cingulum. • P_4 shows bicuspid equal valve (principal and inner cusp). • P_4 complex structure and much more deeply cleft outer cusps. • P_4 separately two main cusps from the talon. 	<ul style="list-style-type: none"> • In the species <i>D. haydeni</i>: M^3 relative longer than <i>Paleochoerus</i>. It also possesses a complicated talon. • This species is distinguished from <i>Sus</i> by the stoutness of the premolars and inferior height of the Talon. 	Canine type is intermediate between verrucosic and scroflic type.	No data
4	<i>Propaleochoerus</i>	<ul style="list-style-type: none"> • P_4 is tall and robust with a deeply cleft summit. • P_1 is reduced 	<ul style="list-style-type: none"> • The labial roots of the upper molars and lingual of lower molars are fused in pair. • Simple quadricusps of upper molar • M^2 Larger than M^3 • M^3 lacking a talon, but talonid developed in the M_3 	<ul style="list-style-type: none"> • Lower canine large and of the verrucosic type. 	<ul style="list-style-type: none"> • U-shaped mandibular symphysis

Continued table 7

No	Genus	Premolar	Molar	Canines	Skull
5	<i>Paleochoerus</i>	<ul style="list-style-type: none"> In the upper or lower last premolar shows bicuspid but in P_4 paracone and metacone not well separated. Talon not developed in P_4 or P^4. P_1 and P_2 not reduced 	<ul style="list-style-type: none"> M^3 has enamel thickness (the lack of hypsodonty). M^3 relative short and wide molars. M^1 relative simple, talon not developed in this genus. In the M^1 and M^2 of <i>P. Paleochoerus</i> though the crest or lobes not as well as visible in general younger genera of Suinae. 	<ul style="list-style-type: none"> Inferior canine of verrucosic type 	<ul style="list-style-type: none"> Zygomatic arch approximately at right angle with the sagittal plane.
6	<i>Hyotherium</i>	<ul style="list-style-type: none"> P_1 and P_2 not reduced P_2 and P_3 have a single cusp, backwardly curved blade-shape cusps. P^4 is very distinctive with two major trenchant cusps. Posteriorly the cingulum is broad and small accessory tubercles. 	<ul style="list-style-type: none"> M_1 and M_2 are simple, rectangular with four major bunodont cusps. Similar in first and second upper molars. The hypoconid is complicated by the growth of accessory tubercles in M_1 and M_2. The cingulum is absent on the lingual surface. 	<ul style="list-style-type: none"> Lower canines is scrofic type The canine has smooth enamel. Upper canines pointing downwards 	<ul style="list-style-type: none"> Well developed sagittal crest in the fronto-parietal areas. The zygomatic process of the maxillary projecting sideways at a right angle to the longitudinal axis of the skull, not developing backward and streamlined as in <i>Sus</i>. Found of juga caninum

Continued table 7

No	Genus	Premolar	Molar	Canines	Skull
7	<i>Metridiochoerus</i>	<ul style="list-style-type: none"> P_1 and P_2 reduced in advanced forms. P_3 simple and mediolaterally flattened bearing one major cusp that linked to the posterior cingulum. P_4 – Tall with single central cusp. Anterior cingulum reduced to single cingulum. Incipient small cusp present between ventral cusp and posterior cingulum. 	<ul style="list-style-type: none"> In M^1/M^2 anterior cingulum prominent with large median pillar. Complex crown pattern in early wear stages. M^3 – Talon lacks symmetry and high variable morphology. 	<ul style="list-style-type: none"> Large, sideways projecting upper canines. Upper canines trefoil cross-section with enamel bands Lower C Verrucosic type. 	<ul style="list-style-type: none"> Wider and slightly concave occipital region with variable median ridge. In lateral profile, the dorsal surface slightly concave The zygomatic process of the maxillary projecting sideways at right angles to the longitudinal axis of the skull. Well-developed angulation of muzzle. Well-developed supra-temporal ridges Wide fronto-parietal region flat lacking sagittal crest Jugum caninum well-developed. Mandible intermediate between V and U shape

Continued table 7

No	Genus	Premolar	Molar	Canines	Skull
8.	<i>Kolpochoerus</i> (<i>Mesochoerus</i>)	<ul style="list-style-type: none"> P₁ and P₂ small P⁴ with 3 major cusps and anterior and posterior cingulum subdivided into small cusps P₄ with additional cusps between main cusp and anterior and posterior cingulum, providing the tooth with a continuous serrate sagittal crest 	<ul style="list-style-type: none"> M³ with talon M₃ with large triangular talonid 	<ul style="list-style-type: none"> Lower C verrucosic type, enamel only on anterior surface Upper C relatively large, projecting upward and forward Upper C covered by enamel on all sides, thinner in progressive forms 	<ul style="list-style-type: none"> Occipital wide and heart-shaped Pronounced angulation of muzzle Zygomatic arch projecting sideways at right angles, lateral border heavily inflated and strongly rugose in males Slightly convex fronto-parietal region, lacking sagittal crest No temporal ridges in early forms, but well-developed in advanced types Jugum caninum present V-shaped symphysis of mandible
9.	<i>Phacochoerus</i>	<ul style="list-style-type: none"> P₁ and P₂ and P¹ and P² reduced P₄--- lacking anterior cingulum, main cusps separated from posterior cingulum by single intermediate cusp. Two distinct of P₄ separated by median pillar. 	<ul style="list-style-type: none"> In M¹/M² distinctly more bilobate. Divided into anterior and posterior lobes. Simple crown morphology M³ – has talon shorter, with fewer pairs of lateral pillar. Well developed median pillars. Less hypodont 	<ul style="list-style-type: none"> Lower C Verrucosic type Large Upper canines Upper canines lacking enamel except on the tip 	<ul style="list-style-type: none"> Cranium with broad zygomatic arches, jugal flares laterally and forms bosses in males Elevated orbits frontal area very broad and flat between orbits. 1 pair of small incisors

No	Genus	Premolar	Molar	Canines	Skull
10.	<i>Celebochoerus</i>	<ul style="list-style-type: none"> P_1 and P_2 and P^1 and P^2 reduced P^4 with 3 major cusps and anterior and posterior cingulum. The P_4 is preserved and has a single triangular cusp with a flat labial and lingual surface. P_4 is about the same width as the M_1 and narrower than the M_2. 	<ul style="list-style-type: none"> M^3 with talon M_3 with small triangular talonid. Very weakly folded enamel, lacking the development of extra lobes, distinct cusps. 	<ul style="list-style-type: none"> Lower C verrucosic type, enamel covered almost on internal and external surface. Upper Canine large, projecting sideward. Upper canine single enamel band below, but may be lacking 	<ul style="list-style-type: none"> Wider and less concave occipital surface. Convex insertion of elevator and rostrii muscles; no concave infraorbital fossa bordered by ridges as in <i>Sus</i>. Zygomatic arch broad and projecting sideways at right angles. Sagittal crest well developed at fronto-parietal areas. Large width of the parietal plane between the temporal fossa. Large tubular alveole for upper canine; lack of jugum caninum Round transverse profile of nasal, no angulation U-shaped symphysis of mandible

11.	<i>Hylochoerus</i>	<ul style="list-style-type: none"> • P_1 and P_2 and P^1 and P^2 reduced 		<ul style="list-style-type: none"> • Lower C Verrucosic type • Large Upper canines • Canines flare broadly outward 	<ul style="list-style-type: none"> • Zygomatic arch robust and expanded, inflated area • Origin levator rostri muscle not bordered by infraorbital ridge; no clearly marked fossa infraorbitalis • Elevated orbits. • Fronto-parietal area wide and concave between orbits • No sagittal crest • Temporal crests strong • occiput wide • Round transverse profile of nasal, no angulation • Large tubular alveole for upper canine; jugum caninum weak • 1 pair of small incisors
12	<i>Potamochoerus</i>	<ul style="list-style-type: none"> • P_1 and P_2 and P^1 and P^2 premolar not reduced. • P^3—broad tooth with a small postero-internal talon and a very slight anterior cingulum. • P^4 show the bicuspid character of the outer lobe and fairly open valley. 	<ul style="list-style-type: none"> • M^3 with talon • M_3 with large triangular talon and more complex. 	<ul style="list-style-type: none"> • Canine relative small 	<ul style="list-style-type: none"> • Skull elongate, pointed and flat from nasals to parietals. • Zygomatic arch projecting sideways at right angles. • Narrow the fronto-parietal region, sagittal crest not developed. • Relative small and concave occipital surface. • Jugum caninum present • V-shaped symphysis of mandible

No	Genus	Premolar	Molar	Canines	Skull
13.	<i>Babyroussa</i>	<ul style="list-style-type: none"> P_1 and P_2 and upper first and second premolar were reduced P^4 with 3 major cusps and anterior and posterior cingulum. The P_4 is preserved and has a single triangular cusp with a flat labial and lingual surface Simple type, less or did not have accessory cusp. 	<ul style="list-style-type: none"> Simple quadricusps of upper molar 	<ul style="list-style-type: none"> Lower C Verrucosic type No enamel band in Upper and Lower canines. Comprising the upper canines, grow upward instead of sideward, penetratting the skin of the snout, and then curving backwards. 	<ul style="list-style-type: none"> Relative small and concave occipital surface. Not well developed of sagittal crest and slightly concave. V-shaped symphysis of mandible. Jugum caninum present
14.	<i>Sus</i>	<ul style="list-style-type: none"> P_1 and P_2 and upper first and second premolar still present P^3 in fossil <i>Sus</i> has well developed anterior internal cingulum. P_4 with elevated anterior and posterior cusps and have a height of talon. 	<ul style="list-style-type: none"> The median valley of M^3 is more complex and accessory cusps present. M_3 with large triangular talonid and have deep radial folds in the main cusps. M_3 the median valley and talonid filled by median cusps or median pillar. 	<ul style="list-style-type: none"> <i>Sus</i> has two type of lower Canine, scrofic and verrucosic type, enamel only on anterior surface. Upper C covered by more than one enamel band Small and medium size of canines 	<ul style="list-style-type: none"> Relative small and concave occipital surface. Not well developed of sagittal crest and slightly concave. V-shaped symphysis of mandible. Jugum caninum present Zygomatic arch projecting streamlines profile not sideways at right angles.

Appendix 4

PALYNOLOGICAL ANALYSIS

<p><i>Sample code : LK-2</i> <i>(Location) : Lakibong, Wallanae</i></p> <p>Member : Burecing Formation : Walanae</p>	<p>13-03-2008 (<i>Date of analysis</i>) Analysed by: Woro Sri Sukapti</p>																																						
General description): organic black clay																																							
Fossil content(s):																																							
<table border="1" style="width: 100%; border-collapse: collapse;"> <tbody> <tr><td><i>Rhizophora</i> type (<i>Zonocostites ramonae</i>)</td><td>113 grains</td></tr> <tr><td><i>Sonneratia alba</i> (<i>Florschuetzia meridionalis</i>)</td><td>22 grains</td></tr> <tr><td><i>Sonneratia caseolaris</i> (<i>F. levipoli</i>)</td><td>30 grains</td></tr> <tr><td><i>Avicennia</i> type</td><td>15 grains</td></tr> <tr><td><i>Barringtonia</i> type(<i>Marginipollis concinus</i>)</td><td>1 grains</td></tr> <tr><td><i>Malvaceae</i> type</td><td>4 grains</td></tr> <tr><td><i>Gramineae</i> (<i>Monoporites annulatus</i>)</td><td>2 grains</td></tr> <tr><td><i>Castanopsis</i> type</td><td>4 grains</td></tr> <tr><td><i>Elaeocarpus</i> type</td><td>27 grains</td></tr> <tr><td><i>Stemonurus</i> type</td><td>16 grains</td></tr> <tr><td><i>Garcinia</i> <i>cuspida</i></td><td>4 grains</td></tr> <tr><td><i>Macaranga</i> type</td><td>2 grains</td></tr> <tr><td><i>Solanum</i> type</td><td>1 grains</td></tr> <tr><td><i>Palmaepollenites</i> sp</td><td>1 grains</td></tr> </tbody> </table>	<i>Rhizophora</i> type (<i>Zonocostites ramonae</i>)	113 grains	<i>Sonneratia alba</i> (<i>Florschuetzia meridionalis</i>)	22 grains	<i>Sonneratia caseolaris</i> (<i>F. levipoli</i>)	30 grains	<i>Avicennia</i> type	15 grains	<i>Barringtonia</i> type(<i>Marginipollis concinus</i>)	1 grains	<i>Malvaceae</i> type	4 grains	<i>Gramineae</i> (<i>Monoporites annulatus</i>)	2 grains	<i>Castanopsis</i> type	4 grains	<i>Elaeocarpus</i> type	27 grains	<i>Stemonurus</i> type	16 grains	<i>Garcinia</i> <i>cuspida</i>	4 grains	<i>Macaranga</i> type	2 grains	<i>Solanum</i> type	1 grains	<i>Palmaepollenites</i> sp	1 grains	<table border="1" style="width: 100%; border-collapse: collapse;"> <tbody> <tr><td><i>Acrostichum aureum</i> type</td><td>10 grains</td></tr> <tr><td><i>Laevigatosporites</i> spp</td><td>43 grains</td></tr> <tr><td><i>Verrucatosporites</i></td><td>15 grains</td></tr> <tr><td><i>Pteris</i> type</td><td>1 grains</td></tr> <tr><td><i>Cyathea</i> type</td><td>2 grains</td></tr> </tbody> </table>	<i>Acrostichum aureum</i> type	10 grains	<i>Laevigatosporites</i> spp	43 grains	<i>Verrucatosporites</i>	15 grains	<i>Pteris</i> type	1 grains	<i>Cyathea</i> type	2 grains
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Age : Not older than Late Miocene																																							
Depositional environment : Mangrove																																							
Index fossils: <i>F. levipoli</i> & <i>F. meridionalis</i>																																							

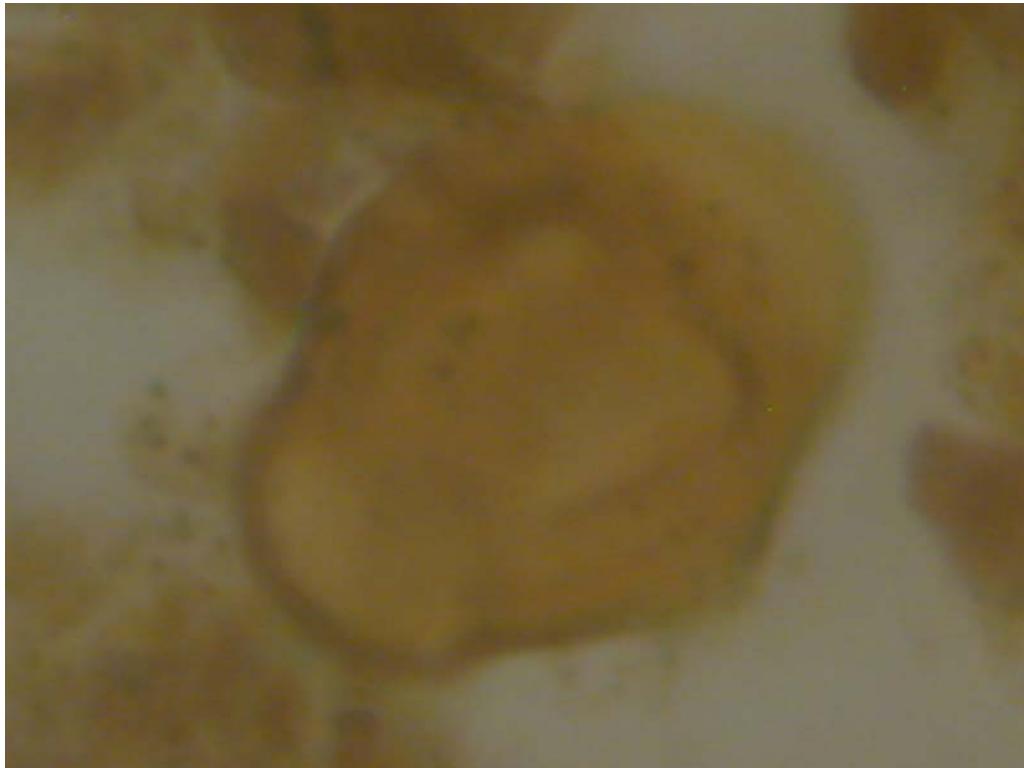
(Sample code) : BRC 28 YN Location: Pompanua road Formation : Walanae Formation	Date of analysis: 20-08-2008 Analysed by : Woro Sri Sukapti
<i>General description:</i> Grey clays	
<i>Fossil content:</i>	
<i>Rhizophora</i> type (<i>Zonocostites ramonae</i>) 4 grains <i>Sonneratia alba</i> (<i>Florschuetzia meridionalis</i>) 1 grains <i>Avicennia</i> type 1grains <i>Corylus</i> type 1grains	<i>Acrostichum</i> 4 grains <i>Laevigatosporites spp</i> 14 grains <i>Verrucatosporites</i> 2 grains <i>Pteris</i> type 2 grains <i>Cyathea</i> type 4 grains
Age : Not older than Late Miocene	
<i>Depositional environment:</i> possible close to mangrove environment	
Fossil index: <i>F. levipoli</i> & <i>F. meridionalis</i>	

(Sample code) : BRC 27 YN Location: Pompanua road Formation : Walanae Formation	Date of analysis: 20-08-2008 Analysed by : Woro Sri Sukapti
<i>General description:</i> tuffaceous clays	
<i>Fossil content:</i> <i>Rhizophora</i> type (<i>Zonocostites ramonae</i>) 5 grains <i>Sonneratia alba</i> (<i>Florschuetzia meridionalis</i>) 3 grains <i>Avicennia</i> type 1 grains <i>Gramineae</i> (<i>Monoporites annulatus</i>) 4 grains <i>Casuarina</i> type (<i>Haloragacidites</i> sp) <i>Retitrricolporites</i> 2 grains grains	<i>Acrostichum</i> 15 grains <i>Laevigatosporites</i> spp 14 grains <i>Verrucatosporites</i> 11 grains <i>Pteris</i> type 2 grains <i>Cyathea</i> type 5 grains
Age : Tidak lebih tua dari Miosen Atas	
Depositional environment : possible close to mangrove environment	
Fossil index : <i>F. meridionalis</i>	

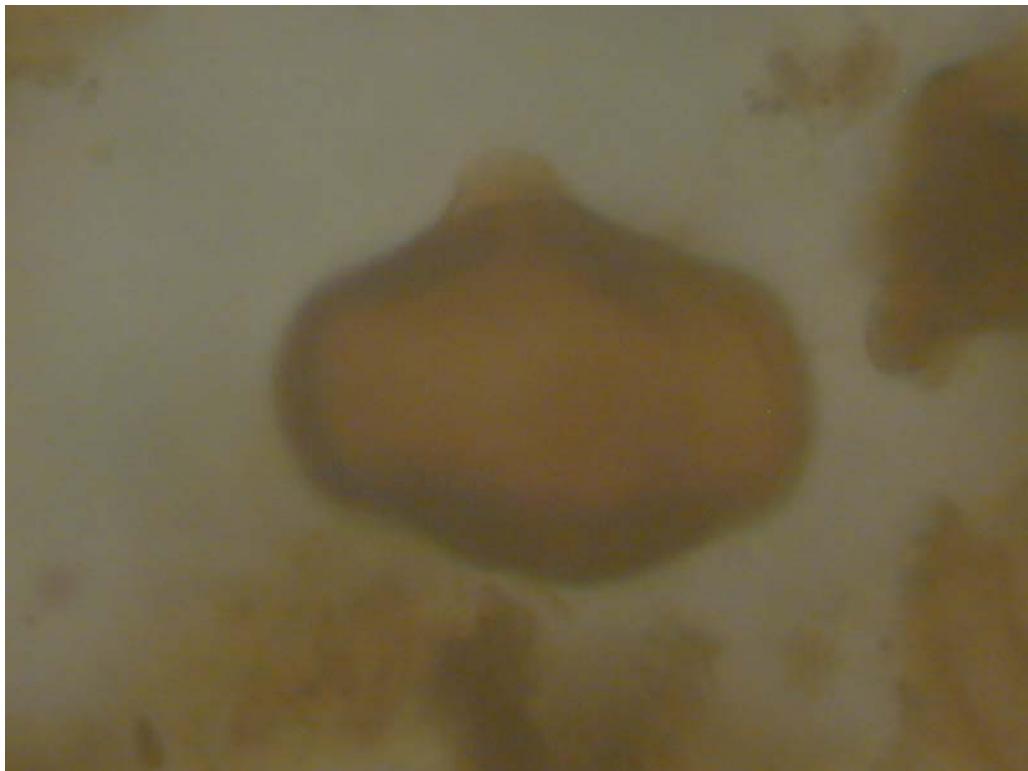
Photo fossil pollen



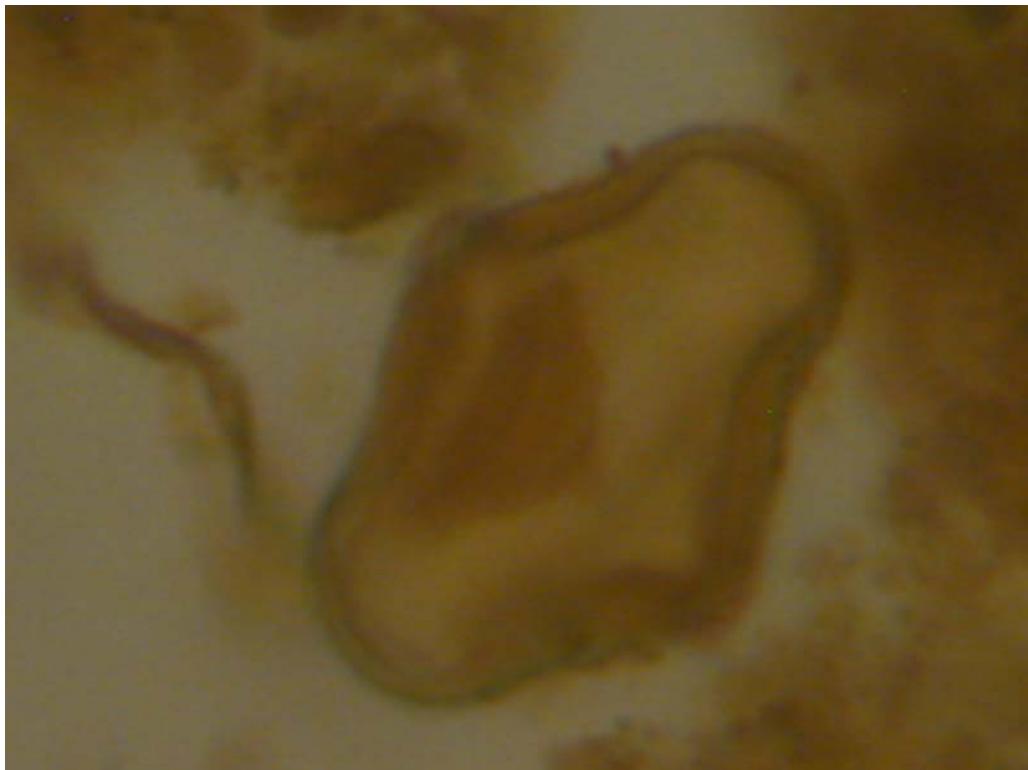
Sonneratia alba (Florschuetzia meridionalis)



Sonneratia alba (Florschuetzia meridionalis)



Sonneratia caseolaris (Florschuetzia levipoli)



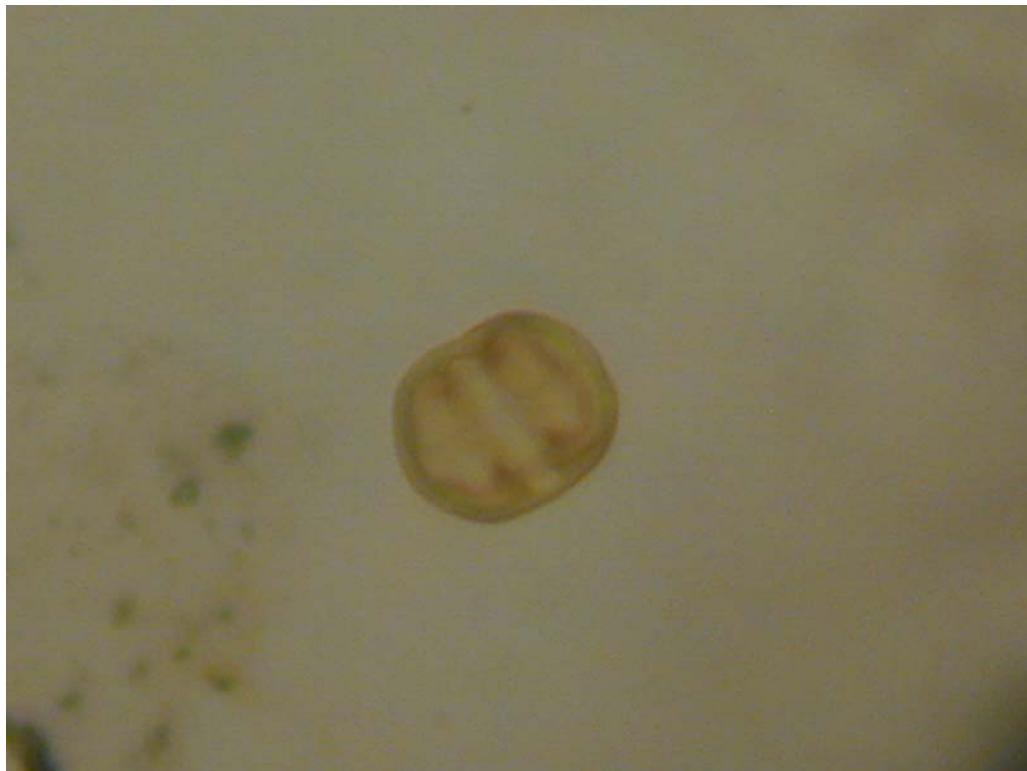
Sonneratia caseolaris (Florschuetzia levipoli)



Barringtonia type(*Marginipollis concinus*)



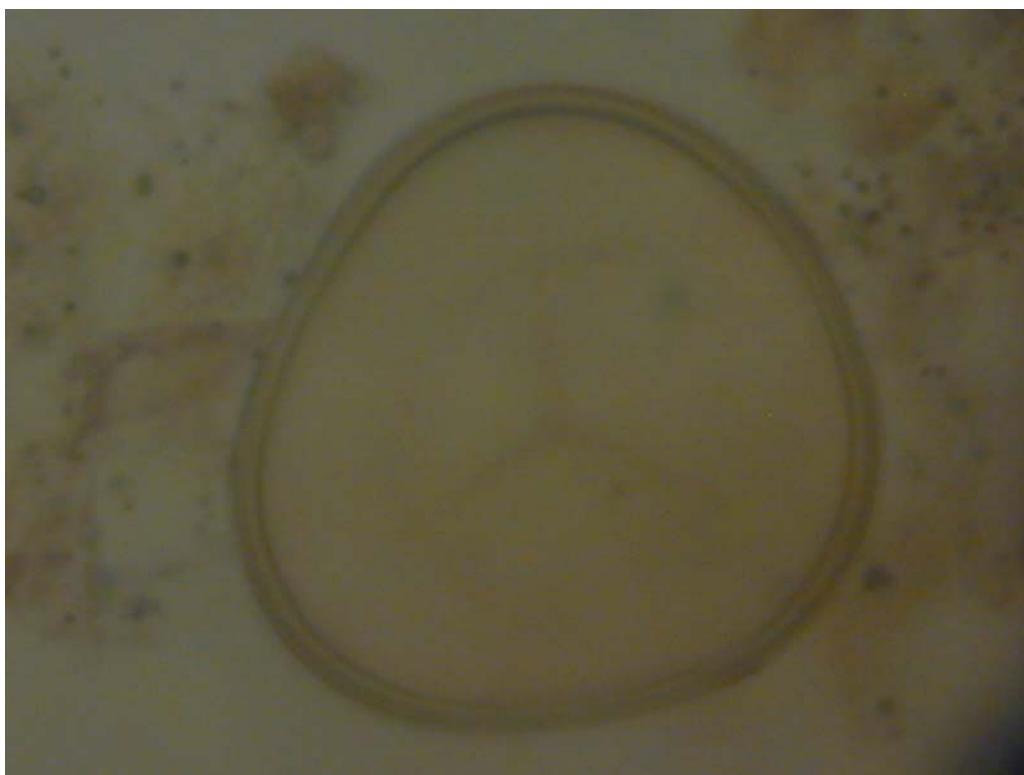
Gramineae (*Monoporites annulatus*)



Rhizophora type (*Zonocostites ramonae*)



Acrostichum



Acrostichum



Laevigatosporites spp



Cyathea type



Pteris type

Appendix 5



Photo1. The Walanae depression is a downfolding, active basin in the north near the study area



Photo2. The Tacipi Member of Walanae Fm is exposed near Jampu along the road Lenrang - Lonrong.



Photo 3. The Burecing Member of Walanae Fm, exposed along the Walanae River near Lakibong, is composed of gray clays locally containing lignite. Pollen from a lignite sample were analysed for a paleo environmental reconstruction.



Photo 4. The Burecing member of Walanae Fm (same area as shown in Photo 3) showing greenish-gray clays interbedded with a shallow marine layer containing molluscs.



Photo 5. Steeply dipping shallow marine clastics of the Samaoling Member of the Walanae Fm exposed in the west flank of the Sengkang Anticline along the road Cabenge - Pompanua.



Photo 6. Samaoling Member, same outcrop as shown in photo 5. A finning upward sequence from medium-grained massive sandstone (right) to an intercalation of thin-bedded fine sand and siltstone layers (left).

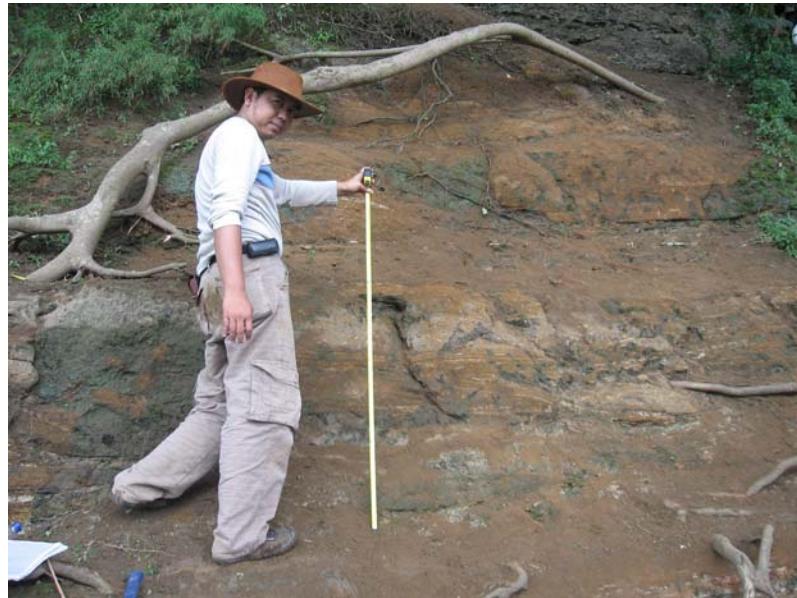


Photo 7. Outcrop on the east bank of the Walanae River near Paroto. Here the transition between the shallow marine Samaoling Member to the deltaic Beru Member is developed as tidally influenced fine-grained sandy layers intercalated with thin mud-drapes that were deposited during slackwater periods.



Photo 8. Outcrop in the west flank of the Sengkang Anticline near Lepangeng, showing medium to coarse-grained fluvial sandstone of the Beru member.

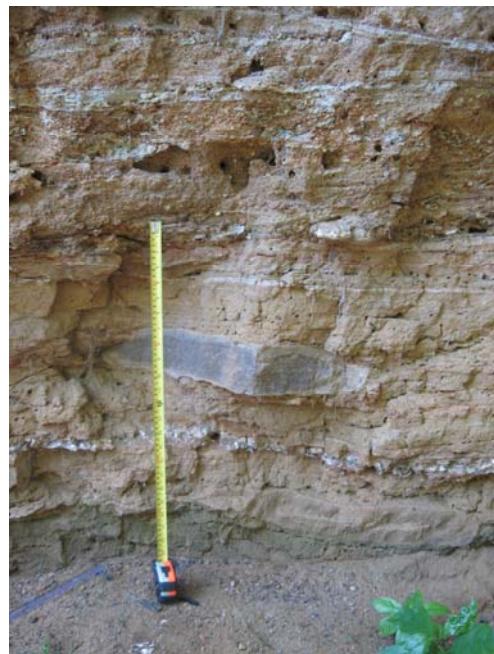


Photo 9. Outcrop near Lenrang, showing fluvial cross-bedded pebbly sandstone of the upper Beru Member.



Photo 10. An upper canine of *Celebochoerus* found in the upper Beru Member at the outcrop shown in photo 9.



Photo 11. Exposure of the Beru Member at Bulu Cepo. Here tidally influenced fluvial sandstones with mud drapes are developed



Photo 12. Outcrop of the Tanrung Fm along the Tanrung River. Cross-bedded pebbly sandstone containing faunal remains are exposed along the coarse of this river.



Photo 13. Cross-bedded alluvial terrace remnant unconformably covering older strata of the Walanae Fm.



Photo 14. A tortoise carapace fragment embedded in fluvial sandstone of the Beru Member near Marale Village.



Photo 15. Tusk fragment in sandy-gravel of the Beru Member
near Marale Village.



Photo 16. Excavation near Lakibong village yielded a large number of *in situ* fossils
From the Beru Member.

Appendix 6

PLATE 1



Explanation:

- Skull fragment of *Celebochoerus heekereni* dorsal view, showing sagittal crest. (Lonrong 2, Coll. GSI No. 0751)
- Left upper canine of *Celebochoerus* (anterior view). (Lonrong, Coll. GSI 0749)
- Maxilla fragment of *Celebochoerus* with M³, M², P⁴ (dextral) and M³–M² (sin). (Lakibong, Coll. GSI No. 2369)
- Maxilla fragment of *Celebochoerus* with sin. P⁴–M¹ (Lonrong, Coll. GSI No. 3569).
- Maxilla fragment of *Celebochoerus* with M³, M², P⁴ (dextral) and M³, M² and P³ (sin). (Lakibong, Coll. GSI No. L2-2365A)
- Sus stremmi* left mandible fragment with m3 (Ngandong, Coll. GSI No. K629)

PLATE 2



Explanation:

- Mandible of *Babyrousa babirussa* male adult (Bumbulan, North Sulawesi; MZB No. 7046) with $P_3 - M_3$ sinistral and dextral
- Skull of *Babyrousa babirussa* male adult (same individual as Fig. A)
- Mandible of *Babyrousa babirussa* male adult (dorsal view) with $P_3 - M_3$ sinistral and dextral and incisor I_1-I_3 (Sulawesi; Coll. MZB No. 15199)
- Skull of adult male of *Babyrousa babirussa*, lateral view (same individual as Fig. C).
- Skull of adult female of *Babyrousa babirussa*, lateral view (Sulawesi; Coll. MZB No. 15201)
- Mandible of *Babyrousa babirussa* adult female with $P_3 - M_3$ sinistral and dextral and incisor I_2-I_3 . Same individual as in Fig. E.