LITERATURE STUDY

The geological history of Sulawesi

Sulawesi is a composite island. It was formed by several collisions of microcontinental fragments from different origins (Hall 1996, 1997, 1998, 2001, 2002). Its eastern and southeastern peninsulas were the margin of the Australian continent, while the southern and northern peninsulas were part of Southeast Asia (Audley-Charles et al. 1972).

Figure 3 gives a reconstruction of South East Asia at 35 and 5 Ma. The figure shows that before 30 Ma, the separation between Asia and Australia was very wide. Starting from 30 Ma, there has been closure of this marine gap (Hall 2001). The southeast part emerged around 20 Ma and was followed not so long after by the emergence of the volcanic north arm (Hall 1998). The western part of Sulawesi was always close to Borneo, although it was largely submerged until at least the late Miocene (Hall 2001). By about 10-5 Ma, there was probably a significant area of land in Sulawesi suitable for animal dispersion.

The mammalian colonization of Sulawesi

"I used to be schizophrenic. But, we are OK now." (Prof. Colin P. Groves 2006, personal communication)

Sulawesi lies in the center of Indo-Australian archipelago, which comprises two zoogeographic realms. Its fauna is a mixture of these realms. To the west, the typical Oriental fauna from many mammalian orders can be found (Groves 1976). This includes Hominoida, Cercopithecidae, Lorisidae, Felidae, Mustelidae, Elephantidae, and other families. This side, comprising Java, Sumatra and Borneo islands, lies on the Sunda shelf, which has a maximum depth of sea of around 60 meters. During period of glaciations in the Pleistocene (Batchelor 1979), the sea level fell world-wide by much more than this depth, so the three islands would have been joined to each other and to the mainland of south-eastern Asia making a uniform land mass (Groves 1976).
Figure 3  Reconstruction of South East Asia at 35 and 5 Ma. Yellow: Eurasian blocks forming Sundaland, red: Australian continental origin blocks, green: mainly volcanic arc, ophiolite, and accreted material (from Hall 1996).
To the east, islands closest to New Guinea, such as Seram and Halmahera, lack the major part of the Oriental fauna (Groves 1976). New Guinea and neighboring islands lie on the Sahul shelf with Australia, and possess a typical Australian fauna such as the Marsupials. These islands, too, are at present separated by a shallow sea.

Today, deep water in all directions separates Sulawesi (including its offshore islands) from other parts of the Indo-Australian archipelago, and most of the Oriental and Australian fauna is missing from this islands. So, how and when did mammals reach Sulawesi?

A land bridge was proposed to connect Java or Borneo to Sulawesi (Bemmelen 1949). This was proposed at a time when plate tectonic movement was unknown. Moreover, it was also uncertain whether there was at any time a complete land bridge from Java or Borneo to Sulawesi. This land bridge would have provided the only entry for large mammals of the Siva-Malayan fauna to Sulawesi (Groves 1976). The Siva-Malayan fauna has been found at two sites in Java: Kali Glagah and Ci Julang, and has been considered as an old faunal stratum. Sometime during the Pliocene the gaps widened keeping out the newer Sino-Malayan fauna (Groves 1976, 1985) from invading Sulawesi.

On the other hand, some workers believe that no evidence for such a land bridge had ever existed (Cranbrook 1981, Musser 1987). The Sulawesi mammals were derived by a sweepstake route across a sea barrier. Back to at least 50 Ma, there was never been a land bridge to Sulawesi (Hall 2001). The only way these animals could get into Sulawesi was by crossing the intervening sea. The plausible time for colonization was at 10-5 Ma (Hall 2001). Although he had proposed a land bridge route earlier, recently Groves (2001) considered the possibility that mammals would have migrated into Sulawesi by rafting when sea level was low, minimizing the distance between Sulawesi and its neighboring islands and making rafting easier.

Origin of Sulawesi macaques

Macaques (monkeys of the genus *Macaca*) exist in Sulawesi. Excluding humans, they are the most widely distributed primates in the world today.
Paleontological findings indicate that macaques already existed in North Africa in the late Miocene (Delson 1980, McIkle 1987), and at the same time dispersed into Europe (Köhler et al. 2000, Rook et al. 2001). They reached China soon after (possibly as early as 5.3 Ma), and Indonesia by the middle Pleistocene (Delson 1980, 1996).

Today, the closest congeneric neighbours of Sulawesi macaques are *M. nemestrina* and *M. fascicularis*. *M. nemestrina* is found on the Malay Peninsula, Borneo, Bangka and Sumatra. Poor fossil evidence suggested that *M. nemestrina* might have existed on Java at one time. There is some consensus that *M. nemestrina* is the sister taxon to all of the Sulawesi macaques based on morphology, mtDNA, and proteins coded by nuclear DNA (Fooden 1969, Cronin et al. 1980, Melnick & Kidd 1985, Fa 1989, Hayasaka et al. 1996, Hoelzer & Melnick 1996, Morales & Melnick 1998). The second species is *M. fascicularis*, which inhabits the Asian continent, Borneo, Sumatra, Java, many offshore islands, the Lesser Sunda Islands (where they have probably been introduced by human agency), and the Philippines. *M. fascicularis* may have dispersed through the Sunda shelf after *M. nemestrina* and encountered different biogeographical opportunities (Fooden 1969, 1976, Eudey 1980, Brandon-Jones 1996). This was confirmed by Evans et al. (1999). They have found that the mtDNA phenetic distances among *M. fascicularis* in Java, Borneo, and the Philippines were small relative to those among *M. nemestrina* in Borneo. These small distances indicate a more recent divergence of *M. fascicularis* than *M. nemestrina* in those areas.

The colonization of Sulawesi by macaques has been estimated to have occurred during the middle Pleistocene (Fooden 1969, Delson 1980, 1996), although Morales & Melnick (1998) and Evans et al. (1999) suggested an earlier date. Initial colonization of central Sulawesi by an ancestor resembling *M. nemestrina* was proposed by Fooden (1969); from this area, radiations spread both south and north. The ancestor was hypothesized to come from Borneo based on the proximity of central Sulawesi with Borneo during low sea level times. He took *M. tonkeana* as the most generalized form based on morphological characteristics such as the suboval form of the ischial callosities, relatively long tail vestige, and relatively unspecialized skull.
Suryobroto (1992) also took *M. tonkeana* as the most generalized species. Using dermatoglyphic pattern types, he proposed four radiations: 1) *M. tonkeana* to *M. nigra*; 2) *M. tonkeana* to *M. maurus*; 3) *M. tonkeana* to *M. hecki* to *M. nigrescens*; 4) *M. tonkeana* to *M. ochreata/M. brunnescens*. He implied that patterns of dispersal did not have to be congruent with the current geography of Sulawesi, as implied by the direct *M. tonkeana* to *M. nigra* radiation.

Close relationships between *M. tonkeana* and *M. nigra* have been demonstrated also by dermatoglyphic analyses by Froehlich *et al.* (1996), by analysis of body color (Hamada *et al.* 1988), and from different hemoglobin beta chain types in these species (Takenaka *et al.* 1987). Evans *et al.* (1999) found *M. tonkeana* that shared derived mtDNA haplotypes with the species from the northern peninsula. Other studies suggest that *M. tonkeana* is not morphologically homogenous throughout its range (Suryobroto pers. comm.). The differences within *M. tonkeana* have stimulated Froehlich & Supriatna (1996) to propose another Sulawesi species in the eastern tip of Sulawesi, *M. togeanus*.

Two species in the northern peninsula, *M. nigra* and *M. nigrescens*, have different morphology from that of *M. tonkeana* (Fooden 1969, Albrecht 1978). Their unique morphology has caused them to be placed in their own separate genus in the past. Diversification of these two species may be a consequence of genetic drift in the north peninsula (Evans *et al.* 1999).

Albrecht (1978) suggested that *M. maurus* is the most generalized form relative to other Sulawesi macaques after measuring their crania. Morphological patterns bifurcate within Sulawesi. A major dispersal was postulated to have spread from *M. maurus* in the southwest peninsula to *M. ochreata* and *M. brunnescens* in the southeast peninsula and distal islands. This dispersal is reflected by the development of narrow and concave supramaxillary ridges in those species. A second dispersal branched north from *M. maurus* into central and northern Sulawesi, now occupied by *M. tonkeana, M. hecki,* *M. nigrescens,* and *M. nigra*. The development of broad supramaxillary ridges of those northern species reflects this second event.

Another candidate for the most generalized form is *M. hecki*. Suryobroto & Iwamoto (1985) had taken *M. hecki* as the pivotal point for diversification of
Sulawesi macaques based on their earlier dermatoglyphic analysis, and Evans et al. (1999) suggested that some mtDNA haplotypes of this taxon are primitive with respect to the other species in northern and central Sulawesi. Close relationship of M. hecki with M. nemestrina from Sabah in northeast Borneo was demonstrated by Harihara et al. (1996) using restriction enzyme analysis of mtDNA.

Another point of view was proposed by Takenaka et al. (1987), who postulated that instead of one event of colonization into Sulawesi, there might be more. This model of multiple dispersal events to Sulawesi was based on the analysis of amino acid sequences of the hemoglobin beta chain in 19 species of macaques. Growing evidence supported this view. Variation in fingerprints of Sulawesi macaques also suggested the same conclusion (Froehlich et al. 1996). They hypothesized that the first dispersal to the northern area of Sulawesi was by M. nemestrina from Borneo, and the second one to the southern area of Sulawesi by M. nemestrina from Java, where it is now extinct. The possibility that a more recent common ancestor of the southern Sulawesi macaques inhabited Java at one time but is now extinct was proposed earlier by Groves (1976, 1980). Additional fossil evidence is needed to support this view.

Evans et al. (1999) proposed another alternative, that the mtDNA haplotypes of Sulawesi macaques was a result of dispersal of M. nemestrina from Borneo to Sulawesi at least twice. One colonization produced the macaques that now occupy the southern peninsula of Sulawesi, which are M. maurus, M. ochreata, and M. brunnescens. Cranial and external morphology of these southern species are similar (Albrecht 1978). The second one reached north or central Sulawesi, perhaps in the southern extent of the range of M. hecki and gave rise to M. hecki, M. tonkeana, M. nigrescens, and M. nigra.

Evidence of multiple origins is also accumulating for other Sulawesi taxa. Evans et al. (1999) cited several works, as mentioned below to strengthen their conclusion. Anoa, a dwarf buffalo, was proposed to have a double dispersal; this was suggested by the difference in the amino acid sequences of the hemoglobin beta chains between lowland and mountain anoa (Kako et al. 1994). Ruedi (1996) supported two colonizations of Sulawesi at different times by shrews, using molecular analysis. Earlier, Somadikarta (1975) explained the morphological
variation in crested tree swifts on Sulawesi also by double dispersal. The proposed times and places of colonization and subsequent dispersal patterns of these taxa, however, are not entirely contemporaneous to the macaque colonization.

Systematics of Sulawesi macaques

There are many proposed taxonomic schemes for Sulawesi macaques. Some have believed that the northern populations are distinct enough morphologically to warrant their own genus, *Cynopithecus* with, in some versions, an additional southeastern genus, *Cynomacaca*. There were also several workers in the past that gave all Sulawesi macaques a genus of their own. The most extreme stand was to include the Sulawesi macaques as a subgenus of the African baboons *Papio*. This was due to the facial appearance of the northern Sulawesi macaques which somewhat resembles the baboon in having prominent supramaxillary ridge (Albrecht 1978).


Their specific status was similarly controversial. Fooden (1969) recognized seven allopatric species of macaques on Sulawesi. These were *M. nigra*, *M. nigrescens*, *M. hecki*, *M. tonkeana*, *M. mauroi*, *M. ochreae*, and *M. brunnescens*. These species differ in a number of external morphological features: (1) tail length, (2) coat coloration, (3) hairy coronal head crest, (4) rump patch, (5) gluteal fields, and (6) ischial callosities. Analysis of craniofacial morphology by Albrecht (1978) later supported specific status of Sulawesi macaques of Fooden (1969). Groves (1980), after making field observations in Sulawesi, concluded that *M. nigrescens* is subspecies of *M. nigra*, *M. hecki* is subspecies of *M.*
tonkeana, and M. brunnescens is subspecies of M. ochreata; but recently he admitted that his 1980’s interpretation is perhaps inappropriate for M. nigrescens and M. hecki (Groves 1997, Brandon-Jones et al. 2004). It was in the days when he believed that the absence of hybridization was the criterion for specific status (Groves pers. comm.).

The systematics of Sulawesi macaques, as presently understood, is:

Order : Primates Linnaeus, 1758
Suborder : Anthropoidea Mivart, 1864 or Haplorhini Pocock, 1918
Infraorder : Catarrhini E. Geoffroy Saint-Hilaire, 1812
Superfamily : Cercopithecoida Gray, 1821
Family : Cercopithecidae Gray, 1821
Subfamily : Cercopithecinae Gray, 1821
Genus : Macaca Lacépède, 1799
Species : M. nigra Desmarest, 1822 (Crested black macaque)
M. nigrescens Temmick, 1849 (Dumog-Bone macaque)
M. hecki Matschie, 1901 (Heck’s macaque)
M. tonkeana Meyer, 1899 (Tonkean macaque)
M. maurus Schinz, 1825 (Moor macaque)
M. ochreata Ogilby, 1841 (Booted macaque)
M. brunnescens Matschie, 1901 (Muna-Butung macaque)


Ischial callosities

Families Hylobatidae and Cercopithecoidae have a pair of non-hairy sitting pads named ischial callosities (Figure 2): thickened skin over the ischial bones and adhering to this bone at the buttock. Within the genus Macaca, the shape of the callosities varies among species, and may be fused across the midline in males (Groves 2000). According to Fooden (1969), the generalized shape of the single callosity is suboval. He also gave descriptions of the callosity for each Sulawesi species using museum specimens. Suryobroto et al. (unpubl. data) tested
Fooden's (1969) typological descriptions by observations of the character's variation directly in Sulawesi, and gave alternative descriptions. Table 1 compares Fooden's (1969) and Suryobroto et al.'s (unpubl. data) descriptions. In *M. nemestrina*, the ischial callosity are suboval, small, and pinkish, or reddish (Suryobroto et al. unpubl. data). No detailed descriptions are available for the callosity of *M. fascicularis*.

<table>
<thead>
<tr>
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<th>Fooden (1969)</th>
<th>Suryobroto et al. (unpubl. data)</th>
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<tbody>
<tr>
<td>1.</td>
<td>suboval, about 3x5 cm of area in males (dry skin), each undivided, pinkish (brownish in dry skins), in MA*</td>
<td>suboval to oblong, small to intermediate, pinkish, yellowish, or darkish pink</td>
</tr>
<tr>
<td>2.</td>
<td>suboval to subreniform, about 3x5 cm of area in males (dry skin), each undivided, dark orange to dark brown (dry skin), in NC*</td>
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<tr>
<td>3.</td>
<td>suboval, about 4x6 cm of area in males (dry skin), each undivided, pinkish in life (pale orange to brownish in dry skins), in TO*</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>suboval, about 4x6 cm of area in males (dry skin), each undivided, pinkish in life (brownish in dry skins), in OC*</td>
<td></td>
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<tr>
<td>5.</td>
<td>suboval to subreniform (dry skin, not seen in living specimens), about 4x6 cm of area in males (dry skin), each undivided, probably pinkish in life (brownish in dry skins), in BR*</td>
<td></td>
</tr>
</tbody>
</table>
2. subreniform to reniform with outward-bending, small to intermediate, pinkish or yellowish
3. subreniform to reniform with inward-bending (maybe weakly subdivided), small to intermediate, pinkish or yellowish
4. reniform with inward-bending, clearly subdivided with upper lobes equal or smaller than lower lobes, big, darkish-yellow to gray
5. reniform with inward-bending, clearly subdivided with upper lobes bigger than lower lobes, big, bright pinkish
6. oblong, protrude, intermediate to big, dark brown

* legend as Figure 1

**Geometric morphometrics**

The description and statistical analysis of shape variation and its covariates is called morphometrics (Bookstein 1991). This field is currently undergoing some change in its methodology (Rohlf & Marcus 1993). Traditionally, morphometrics has been based largely on multivariate analysis of homologous linear distances, angles, ratios, and areas. Because of its scalar characteristics, basically the measurements reflect size, not shape, of the organisms. This approach lacks the ability to depict graphically the shape differences between forms, but offers many advantages to plot individual data onto hyperdimensional character space. For example, it is difficult to picture the actual shape change from
principal component coefficients, or it is hard to depict the shape differences between groups of specimens from canonical variate analysis plots. In the new methods, the analytical framework of data collection shifted from scalar measurement to Cartesian (x, y or even x, y, z for 3 dimensions) coordinates of anatomical landmarks from biological form. Given an optimum numbers of landmark outlining the form, the coordinate data will sufficiently represent the shape. This method is called geometric morphometrics.

There are several tools developed for use in geometric morphometrics, which are superimpose and deformation analysis tools. Rohlf and Slice (1990) offered a superimpose formula that can line up all coordinates of shapes to their common centroid. Each coordinate is then rotated according to a criterion to minimize the shape variation among them. This is called Generalized Procrustes Analysis (GPA) and formerly was called Generalized Least Squares (GLS). This tool is useful because it can be used to calculate an average shape of a biological group. This average shape then can be treated as a typical shape of that group, or it can be utilized as a referential shape for deformation analysis.

Deformation analysis began when Thompson (1917) developed a method to produce deformation grids, in which a square grid is drawn over one form and then smoothly deformed to produce a second form. The pattern of grid deformation describes the shape change. Thompson drew the grids by hand so the results were somewhat subjective, although this did not prevent them from appearing in many anthropology and primatology textbooks. Bookstein (1991) developed statistical techniques that allow the deformation grid to be drawn objectively. It is called Thin-plate Splines (TPS). It allows description of deformation of one form (usually a reference form) onto another, using movements of landmarks. This process will generate grids that demonstrate the mapping of homologous landmark of the two forms. Full technical and mathematical backgrounds of this method can be found in Bookstein (1991).

The TPS decompose shape difference into an affine and a non-affine component, which can be shown as a deformation grid. The affine (also called linear or uniform) component retains parallel lines in the deformation grid; it represents global shape change, which occurs equally across all landmarks and is
produced by differences in size, orientation, or location between two forms. The non-affine (also called non-uniform) component represents the remaining change, which is specific to certain area composed by a subset of landmarks and so allows the researcher to identify localized changes of the form under study. Further, the non-affine component can be decomposed to reveal partial warps of the potential change of the reference form; the partial warp scores are the shape descriptors of a given form. The level of deformation from a reference to this given form is expressed by a shape-space metric called bending energy. It will take more energy to move two landmarks that are close to each other than relatively separated ones. Affine deformation requires zero bending energy, whereas the non-affine components require successively larger amounts of bending energy at successively smaller, more local scales of deformation.

In order to summarize variation in non-affine components, principal component analysis of partial warp scores can be performed to generate several orthogonal dimensions, which is called relative warps. Rohlf (1993) give full mathematical background of relative warps (RW). Each RW carries a proportion of variance contained in the non-affine components. The first RW carries the biggest proportion and the remaining RWs carry parts of variance in a progressively smaller proportions. Therefore, RWs can be used to extract general tendencies of variation in non-affine components. Brief mathematical formulae of geometric morphometrics tools used in this research can be found in Appendix 1.