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External Characteristics and Associated Developmental Changes in Two Species of Sulawesi Macaques, *Macaca tonkeana* and *M. hecki*, with Special Reference to Hybrids and the Borderland Between the Species

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ABSTRACT. The degree of intergradation between two species of Sulawesi macaques, *Macaca tonkeana* and *M. hecki*, was studied by examining the diagnostic external characteristics of more than 100 monkeys kept as pets by natives. Two possible hybrid monkeys were found and both originated from the borderland between the two species, located in the most proximal region of the northern peninsula of Sulawesi. The previously postulated wide area of intergradation between the two species at the possible contact zone was, however, not recognized, and typical examples of *tonkeana* or *hecki* were found to be present on the two sides of a narrow "hybrid" zone which was defined by direct observations. Furthermore, despite considerable individual variations, we were able to allocate most monkeys to one or other of the species. Each of ten external characteristics of the members of both species more or less encompassed the individual variations, but may undergo changes with the development of the monkeys. The mechanisms of reproduction of hybrid monkeys and the maintenance of differences between the species are discussed.

Key Words: *Macaca tonkeana*; *Macaca hecki*; Hybrid; Sulawesi macaque; Developmental change; External characteristics.

INTRODUCTION

Sulawesi macaques include several species that live allopatrically and contiguously with one another. In his classic study on Sulawesi macaques, FOODEN (1969) indicated that the Sulawesi macaques can be classified into seven species by well-defined phenotypes. FOODEN's seven species of Sulawesi macaques are as follows: *Macaca maura* on the southern peninsula, *M. brunnescens* on the islands of Buton and Muna, *M. ochreata* on the southeastern peninsula, *M. tonkeana* in the central region of Sulawesi, *M. hecki* in the proximal region, *M. nigrescens* in the middle region, and *M. nigra* at the distal end of the northern peninsula. It has been suggested that the differences between the various species of Sulawesi macaques are similar in magnitude to those exhibited by all of the non-Sulawesi macaques, although the geographical range of the Sulawesi macaques occupies less than 2% of the total area inhabited by macaques (ALBRECHT, 1978). In general, the southern species tend to exhibit more generalized characteristics and the northern species to exhibit more specialized characteristics (ALBRECHT, 1978; FOODEN, 1969; HILL, 1974). Furthermore, these seven species may be the result of endemic radiation within the island from a single ancestral stock, similar to the species of the *M. leonina-nemestrina* group which originated from the Sunda shelf in the middle Pleistocene (FOODEN, 1969).

At present, no physical boundary exists to inhibit the movement of macaques between the regions occupied by most of those neighboring species mentioned above. It is necessary therefore to determine whether or not there are hybrids or intermediate forms derived from neighboring species. The natural occurrence of a hybrid would apparently contradict the biological species criterion of reproductive isolation (MAYR, 1963). After a brief survey of pet monkeys kept by natives in the borderlands, GROVES (1980) found some possible examples of hybrids between *M. tonkeana*, and *M. hecki* and between *M. nigrescens* and *M. nigra*. He classified *M. hecki* as a subspecies of *M. tonkeana*, and *M. nigrescens* as a subspecies of *M. nigra*. Due to a lesser degree of diversification, *M. brunnescens* was also classified as a subspecies of *M. ochreata*, even though these two species are separated geographically by the sea which lies between the southeastern peninsula and offshore islands. According to GROVES (1980), two particular species, *M. tonkeana* and *M. hecki*, clearly illustrate the diversity of intergradation patterns at the borderland near the base of the northern peninsula.

Since 1981, surveys of pet monkeys have been carried out several times by a Japanese research team (HAMADA et al., 1988; KAWAMOTO et al., 1982, 1985, 1987; TAKENAKA et al., 1987a, b). During these surveys, more than 400 pet monkeys belonging to all the species of Sulawesi macaques were examined all over the island. Almost all of the pet monkeys inspected could be readily designated as a member of one of FOODEN's seven species based on an assessment of their external characteristics, and monkeys that displayed intergradations between the relevant species were rather few in number. The same results held true even at the borderland of *M. tonkeana* and *M. hecki*. GROVES (1980) was able to examine only 16 monkeys in this area, possibly because of the very short period of time available, and was therefore unable to evaluate the local variations and developmental changes. Furthermore, the information available to the Japanese survey team was also limited because few pet monkeys originated from this borderland.

An intensive survey of pet monkeys of *M. tonkeana* and *M. hecki* was therefore carried out with the aim of clarifying the degree of intergradation and the boundary between these two species. This survey was made independently of the other Japanese team members. The present report thus describes the results of an examination of about 100 pet monkeys throughout the ranges of both species, with the emphasis on the borderland between them. Developmental changes in the external characteristics and some local variations are also analyzed. In addition, the results of brief field observations made at the borderland are presented.

METHODS

An intensive survey was carried out from September 23 to October 31, 1988, and 88 pet monkeys were inspected. These monkeys came from most areas within the ranges of both species. Fourteen other monkeys were inspected and their external characteristics, recorded by chance by the first author, were also included in the analysis. Many people in Sulawesi keep monkeys as pets and they can usually provide information about the origin of their pets, as mentioned by GROVES (1980). However, in some cases, the precise location of the place of original capture of the pet monkey remains obscure due to repeated transfers between owners, and the stated origin could involve some misunderstanding by the owners and/or may reflect recent disturbances of the physical environment by humans. For instance, we found a typical *M. tonkeana* at the boundary of *M. hecki* and *M. nigrescens*,

east of Gorontalo City, and a typical *M. hecki* at the boundary of *M. nigrescens* and *M. nigra*. The owners testified that both monkeys were captured in the nearby forests when still young. After discussing the situation prevailing at the time when the owners captured their pets, it was found that these monkeys had in fact been captured in their original babitats and then moved and released at their respective places of recapture. Furthermore, some monkeys were captured in villages or even within the city, and may thus have escaped from their previous owners. One monkey was reported to have been caught after it had jumped from a moving car which then disappeared. The information provided by the owner could not therefore be accepted at face value in some cases. However, almost all owners of pet monkeys were able to tell us the original site of capture of their pets, although they usually gave the name of the place in which the people who caught the pet monkeys lived rather than that of the place where the relevant monkeys were actually captured.

It was clear that the origin of the pet monkeys became more obscure after many transfers between owners. It was necessary therefore to examine monkeys as near to their original habitats as possible and to obtain information from their first owners, who might have actually captured the monkeys. Accordingly, we used a car to travel around and between villages and made an effort to locate the pet monkeys near their original habitats. Also, inspection of monkeys in Palu, the capital city of Central Sulawesi Province, was restricted because of the vagueness of the available information. We noted the "information fidelity" for the pet monkeys when we examined them, as follows: "A" refers to a pet monkey which was captured by the owner himself or a member of his own family; "B" refers to a monkey transferred once from its original owner to the present owner; "C" refers to a monkey belonging to a person who could state its origins with some certainty; and "D" refers to a monkey which may have been transferred several times between owners. Of the 102 pet monkeys inspected by us, 39 individuals were in category "A," 29 individuals in "B," 18 individuals in "C," and 16 individuals (including 7 of unknown origin) in "D." These criteria depended completely on the statements by the owners, so that there could be some mistakes even in criteria "B" or "C." However, in most cases, we were able to obtain reliable information on the original sources of the pet monkeys.

The method employed to evaluate the degree of intergradation between *M. tonkeana* and *M. hecki* was identical to that adopted by GROVES (1980). Ten external characteristics were used to discriminate between the two species, and intermediate states were scored between 1.0 (*tonkeana*-type) and 0.0 (*hecki*-type). The pet monkeys could thus be scored from 10.0 (typical *tonkeana*) to 0.0 (typical *hecki*). The chosen differences in external characteristics between *M. tonkeana* and *M. hecki* were as follows: (1) *M. tonkeana* has pale grayish cheek-whiskers, while *M. hecki* lacks wiskers and simply has brownish hair which may be lighter to some extent on the cheeks than on the other parts of the head. (2) The underpart of *hecki* is distinctly paler than the upperside, but this is not the case in *tonkeana*, although many monkeys of *tonkeana* do have a pale-grayish chest and axillae. (3) The forearms of *hecki* are dark brown but those of *tonkeana* are black. (4) The shanks of the hindlegs are distinctly light-brownish in *hecki* but black in *tonkeana*. (5) *M. tonkeana* has a wide and pale-grayish rump patch, while that of *hecki* is not sharply delineated, although it is lighter than the dorsum. (6) The rump patch of *tonkeana*, but not of *hecki*, is covered by dense and bushy hairs. (7) "Gluteal fields," i.e. bare or tiny-haired areas on either side of the tail, are conspicuous in *tonkeana*, but virtually absent in *hecki*. (8) The ischial callosities of *tonkeana* are oval, while those of *hecki* are reniform and the upper and lower lobes are separated medially by a transverse crease. (9) The ischial callosity of *hecki* is gray-yellow, while that of *tonkeana* is orange-colored. It should be noted that the callosity of *tonkeana*

is readily stained and, in many cases, it looks blackish for the most part. It is often difficult therefore to distinguish its color without cleaning; such a condition was never observed in the other species of Sulawesi macaques. (10) The tail of *hecki* is tiny and stub-like. The tail of *tonkeana* is much longer, but is still very short compared to the tails of most other extant non-Sulawesi macaques.

These external characteristics were scored individually for each pet monkey examined, as follows: (1) Color of cheeks: dark, 0; light-tipped, 0.3; medium gray-brown, 0.7; pale, 1.0. (2) Color of ventral surface: distinctly paler than dorsal part, 0; slightly paler, 0.5; dark, 1.0. (3) Color of forearms: darkish brown, 0; brown tones, 0.5; black, 1.0. (4) Color of external surface of hind-shanks: gray-brown, 0; somewhat browner/grayer than thighs, 0.3; brown traces, 0.7; black, 1.0. (5) Color of rump patch: dark, 0; gray or buff, 0.5; pale buff, 1.0. (6) Crest of rump patch: absent, 0; intermediate, 0.5; conspicuous, 1.0. (7) Gluteal fields: very small or absent, 0; intermediate, 0.5; large, 1.0. (8) Shape of ischial callosity: reniform, 0; oval but weakly recognizable as reniform, 0.5; oval, 1.0. (9) Color of ischial callosity: gray-yellow, 0; pinkish, 0.5; pinky orange, 1.0. (10) Tail: stub, 0; intermediate, 0.5; *tonkeana*-length, 1.0.

The scoring system of GROVES (1980) was thus followed exclusively and without any modifications. However, since no standardizations had been made beforehand, the scores assigned to each external characteristic were absolutely dependent on our own judgement. Since these external characteristics may include very subtle differences between individual monkeys, different scoring by different researchers was inevitable. In some cases, it was necessary for us to discuss the scores until a final score could be agreed upon.

All 102 pet monkeys inspected were classified as either *M. tonkeana* or *M. hecki* based on their external characteristics. As mentioned above, almost all the monkeys could be allocated to one of the two species, although it was rather rare for the monkeys to receive a perfect score [that is, typical *tonkeana* (10.0) or typical *hecki* (0.0)] and it was difficult to ascertain the species of some infants since infants lack advanced characteristics. The developmental changes in each external characteristic were analyzed for each species. We found only two monkeys with clearly intermediate character scores, and they came from the possible borderland between the two species. We therefore carried out some preliminary field observations for a week, using a Nikon Fieldscope (20 ×), in this borderland to ascertain the presence of hybrids and to examine how they live in the natural habitat.

RESULTS

The scores of all pet monkeys inspected are shown in Table 1 with the allocated species in each case. As is apparent from these data, a few pet monkeys had external characteristics typical of one or other of the two species, *M. tonkeana* or *M. hecki*, irrespective of their stated origins. It is also worthy of note that individual variations could be recognized in monkeys from areas far from the borderland. In fact, the borderland of these two species can be clearly defined from these data as the narrow area at the base of the northern peninsula, from near Kebon Kopi to Toboli, where the only route from the east to the west coast crosses the peninsula (Fig. 1). Two monkeys (*No. 18* from Watatu and *No. 21* from Palopo) apparently contradict the patterns of distribution of these two species: they are rather typical examples of *M. hecki* despite their cited origins within the range of *M. tonkeana*. The owners of *No. 18* and of *No. 21* insisted that these monkeys were captured in the nearby forests. However, these monkeys had been transferred between owners several times prior

Table 1. Monkeys examined and scoring of their external characteristics. (For footnotes see Page 67)

No.	Where seen	Stated origin	I.F.[1)]	Age/sex[2)]	Color of cheeks	Color of ventral surface	Color of fore-arms	Color of hind-shanks	Rump patch: color	Rump patch: crest	Gluteal fields	Ischial callosity: shape	Ischial callosity: color	Tail length	Score	Judged species
1	Toili	Toili	A	Inf F	—	1.0	1.0	1.0	1.0	1.0	0.0	1.0	0.5	1.0	7.5~	*M. tonkeana*
2	Luwuk	P. Peleng	C	Juv-s F	1.0	0.5	1.0	0.7	1.0	1.0	0.0	1.0	1.0	1.0	8.2	*M. tonkeana*
3	Luwuk	Luwuk	B	Ad M	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
4	Luwuk	Luwuk	C	SAd F	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	10.0	*M. tonkeana*
5	Luwuk	Luwuk	A	Juv-l M	0.3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	8.8	*M. tonkeana*
6	Luwuk	Luwuk	A	Juv-l M	0.0	1.0	1.0	0.7	1.0	1.0	0.5	1.0	0.5	1.0	7.7	*M. tonkeana*
7	Biak	Lamala	B	Juv-s F	0.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	8.5	*M. tonkeana*
8	Biak	Wedikan	A	Juv-s F	0.3	0.5	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	8.5	*M. tonkeana*
9	Biak	Lamala	B	Juv-l F	0.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	8.5	*M. tonkeana*
10	Luwuk	Balantak	C	Ad F	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	10.0	*M. tonkeana*
11	Lembasada	Lembasada	B	Juv-l M	0.3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.3	*M. tonkeana*
12	Lalombi	Lalombi	B	Juv-s M	0.3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.3	*M. tonkeana*
13	Sintubu	Sintubu	A	Juv-s M	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.0	*M. tonkeana*
14	Kamarora	Kamarora	B	Juv-l M	0.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	8.5	*M. tonkeana*
15	Kamarora	Knarom	A	Juv-s M	0.3	1.0	1.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	8.8	*M. tonkeana*
16	Bangga	Bangga	A	SAd M	0.7	1.0	1.0	1.0	0.5	1.0	1.0	1.0	1.0	1.0	9.2	*M. tonkeana*
17	Bangga	Bangga	A	Inf M	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.0	*M. tonkeana*
18	Balane	Watatu	D.	Ad M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	*M. hecki*
19	Balane	Lewara	B	Juv-s M	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.0	*M. tonkeana*
20	Bilomaru	Palolo	D	Juv-l F	0.3	1.0	1.0	1.0	0.5	1.0	1.0	1.0	1.0	1.0	8.8	*M. tonkeana*
21	Bilomaru	Palolo	D	SAd M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	*M. hecki*
22	Kalawara	Toaya	A	Ad F	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.0	1.5	*M. hecki*
23	Kalawara	Kalawara	B	SAd F	0.7	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
24	Watukilo	Watukilo	A	Ad M	0.7	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
25	Lampeleo	Lampeleo	A	SAd F	0.3	1.0	1.0	1.0	0.5	1.0	1.0	1.0	0.5	1.0	8.3	*M. tonkeana*
26	Sapoh	Sapoh	A	Inf M	0.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	0.5	1.0	8.0	*M. tonkeana*
27	Omu	Donggulu	A	Juv-s M	0.0	0.5	0.5	0.0	0.0	0.5	0.5	0.0	0.5	0.0	2.5	*M. hecki*
28	Pandere	Pandere	A	Ad F	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	*M. tonkeana*
29	Pandere	?	D	Ad M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	2.0	*M. hecki*
30	Pandere	Pandere	A	Ad M	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
31	Pandere	Pandere	A	Ad M	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
32	Pandere	Gimpu	C	Juv-s M	0.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	1.0	1.0	8.5	*M. tonkeana*
33	Kalawara	?	D	Juv-s F	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	8.5	*M. tonkeana*
34	Kalawara	Enu	A	Juv-l F	0.0	0.0	1.0	0.0	0.0	0.0	0.5	0.0	0.5	0.5	2.5	*M. hecki*
35	Sidondo	Sidondo	C	Juv-s M	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.0	*M. tonkeana*
36	Dupa Tondo	Kebon Kopi	B	Juv-l M	0.0	0.5	0.5	0.0	0.0	0.5	0.5	1.0	0.5	0.5	4.0	*?M. hecki*
37	Batutela	Batutela	A	SAd M	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.0	*M. tonkeana*
38	Tawaei	Marantale	C	Juv-l M	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	*M. hecki*
39	Tolai	Sukusade	C	Ad F	0.0	1.0	1.0	1.0	—	—	1.0	1.0	0.5	1.0	6.5~	*M. tonkeana*
40	Tolai	Sausu	B	Ad M	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	10.0	*M. tonkeana*

(continued)

Table 1. (continued)

No.	Where seen	Stated origin	I.F.[1)]	Age/sex[2)]	Color of cheeks	Color of ventral surface	Color of fore-arms	Color of hind-shanks	Rump patch: color	Rump patch: crest	Gluteal fields	Ischial callosity: shape	Ischial callosity: color	Tail length	Score	Judged species
41	Tolai	Lambunu	B	SAd M	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	*M. hecki*
42	Tolai	Tolai	B	Juv-s M	0.3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.3	*M. tonkeana*
43	Tanalanto	Tanalanto	A	SAd M	0.3	1.0	1.0	0.3	1.0	1.0	1.0	1.0	0.5	1.0	8.1	*M. tonkeana*
44	Tanalanto	Ongka	C	Ad F	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	1.0	*M. hecki*
45	Tanalanto	Ongka	C	Ad F	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.0	1.5	*M. hecki*
46	Sumbarsari	Toboli	A	Ad F	0.7	1.0	1.0	1.0	0.5	0.5	1.0	1.0	0.0	0.0	6.7	*?M. tonkeana*
47	Sumbarsari	Poso	D	SAd M	1.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	0.0	0.5	8.0	*M. tonkeana*
48	Panbalowo	Lambunu	B	Inf M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	2.5	*M. hecki*
49	Parigi	Tindaki	B	Ad M	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
50	Parigi	Olaya	A	Ad F	0.7	1.0	1.0	0.7	0.5	0.5	1.0	1.0	1.0	1.0	8.4	*M. tonkeana*
51	Silanga	Silanga	A	Juv-s M	0.7	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	9.2	*M. tonkeana*
52	Ampibabo	Silanga	D	Juv-l M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	*M. hecki*
53	Pinotu	Pelawa	C	Ad M	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
54	Laemanta	Laemanta	A	Juv-s M	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.5	1.5	*M. hecki*
55	Kasimbar	Kasimbar	B	Ad F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	*M. hecki*
56	Kotaraya	Kotaraya	B	SAd M	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	*M. hecki*
57	Kotaraya	Kotaraya	B	Juv-s F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*M. hecki*
58	Ogotumbu	Lambunu	B	Juv-l M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	*M. hecki*
59	Tomini	Tomini	A	Juv-l M	0.0	0.5	0.5	0.0	0.0	0.5	0.0	0.0	0.0	0.0	1.5	*M. hecki*
60	Lemusa	Lemusa	A	SAd M	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	10.0	*M. tonkeana*
61	Lemusa	Lemusa	A	Ad F	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	10.0	*M. tonkeana*
62	Lemusa	Sausu	A	Ad F	0.7	1.0	1.0	0.3	1.0	1.0	1.0	1.0	1.0	1.0	9.0	*M. tonkeana*
63	Parigimpu	Parigimpu	A	Juv-s M	0.3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	8.3	*M. tonkeana*
64	Tondo	?	D	Juv-s M	0.7	0.5	1.0	0.3	1.0	1.0	1.0	1.0	1.0	1.0	8.5	*M. tonkeana*
65	Dalaka	Poso	D	Ad M	1.0	1.0	1.0	0.3	1.0	1.0	1.0	1.0	1.0	1.0	9.3	*M. tonkeana*
66	Labuan	Labuan	A	Juv-l M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	*M. hecki*
67	Patigo	Toboli	B	Inf M	0.7	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	1.0	9.2	*M. tonkeana*
68	Maleni	Maleni	A	Juv-s M	0.7	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.4	*M. tonkeana*
69	Watusampu	Watusampu	A	Ad F	1.0	—	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0	8.0~	*M. tonkeana*
70	Boyaoge	?	D	Ad M	0.0	0.5	1.0	0.3	0.0	0.5	0.0	0.0	0.0	0.0	2.3	*M. hecki*
71	Tamarenja	Batusuya	B	Juv-l F	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.0	1.5	*M. hecki*
72	Tj. Padang	Sibado	B	Ad M	0.0	0.5	0.5	0.0	0.0	0.5	0.0	0.0	1.0	0.0	2.5	*M. hecki*
73	Sipi	Sipi	B	Juv-s M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	2.5	*M. hecki*
74	Sipi	Sipi	A	Inf F	0.0	0.5	1.0	0.3	0.0	0.0	0.0	1.0	0.5	0.5	3.8	*M. hecki*
75	Tompe	Tompe	B	Inf M	0.0	0.5	1.0	0.3	0.0	0.0	0.0	1.0	1.0	0.0	3.8	*M. hecki*
76	Sibado	Sibado	A	Inf F	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.5	1.0	0.0	2.5	*M. hecki*
77	Talaga	Talaga	A	Inf M	0.0	1.0	1.0	0.3	0.0	0.0	—	1.0	0.5	0.5	4.3~	*M. hecki*
78	Sioyong	Sioyong	B	Inf M	0.0	0.5	1.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	2.5	*M. hecki*
79	Malonas	Malonas	B	Inf M	0.0	1.0	1.0	0.3	0.0	0.5	0.0	1.0	1.0	0.0	4.8	*M. hecki*
80	Batusuya	Batusuya	A	Juv-s F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.5	0.0	1.0	*M. hecki*

(continued)

Table 1. (continued)

No.	Where seen	Stated origin	I.F.[1]	Age/sex[2]	Color of cheeks	Color of ventral surface	Color of fore-arms	Color of hind-shanks	Rump patch: color	Rump patch: crest	Gluteal fields	Ischial callosity: shape	Ischial callosity: color	Tail length	Score	Judged species
81	Wani	Leok	C	Ad M	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	*M. hecki*
82	Palu	?	D	Ad F	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	10.0	*M. tonkeana*
83	Palu	?	D	Juv-s M	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.5	0.5	0.0	3.0	*M. hecki*
84	Palu	?	D	Ad M	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	9.5	*M. tonkeana*
85	Donggala Kodi	Donggala Kodi	A	Ad F	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
86	Donggala Kodi	Tentena	C	Ad M	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	1.0	1.0	9.7	*M. tonkeana*
87	Palu	Watatu	C	SAd M	0.3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	9.3	*M. tonkeana*
88	Gorontalo	Batudaa	D	Juv-s F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.5	*M. hecki*
89	Timbuolo	Timbuolo	B	Ad M	1.0	1.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	1.0	9.5	*M. tonkeana*
90	Gorontalo	Papayato	C	Juv-s M	0.0	1.0	1.0	0.5	0.0	0.0	0.0	0.0	0.5	0.0	3.0	*M. hecki*
91	Dunbayabulang	Antingola	C	Juv-s M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*M. hecki*
92	Duano	Marisa	D	Ad M	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	*M. hecki*
93	Boidu	Pohe	B	Juv-l M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	*M. hecki*
94	Tupa	Longalo	A	Juv-s F	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	2.5	*M. hecki*
95	Buhu	Malalafu	C	Ad F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*M. hecki*
96	Pinolosian	Pinolosian	A	SAd M	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	*M. hecki*
97	Isimu	Paguyaman	C	Juv-s M	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	*M. hecki*
98	Isimu	Paguyaman	C	Ad F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*M. hecki*
99	Kayuboko	Parigi	D	Juv-s	0.0	—	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	8.0~	*M. tonkeana*
100	Papanga Parigi	Ongka	B	Ad F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	*M. hecki*
101	Kalibru	Batusuya	B	Ad F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*M. hecki*
102	Lambunu	Lambunu	A	Inf F	0.0	1.0	1.0	—	0.0	0.0	—	1.0	0.5	0.0	3.5~	*M. hecki*

1) Degree of information fidelity (see text); 2) Inf: infant; Juv-s: small juvenile; Juv-l: large juvenile; SAd: Subadult; Ad: adult. M: Male; F: female.

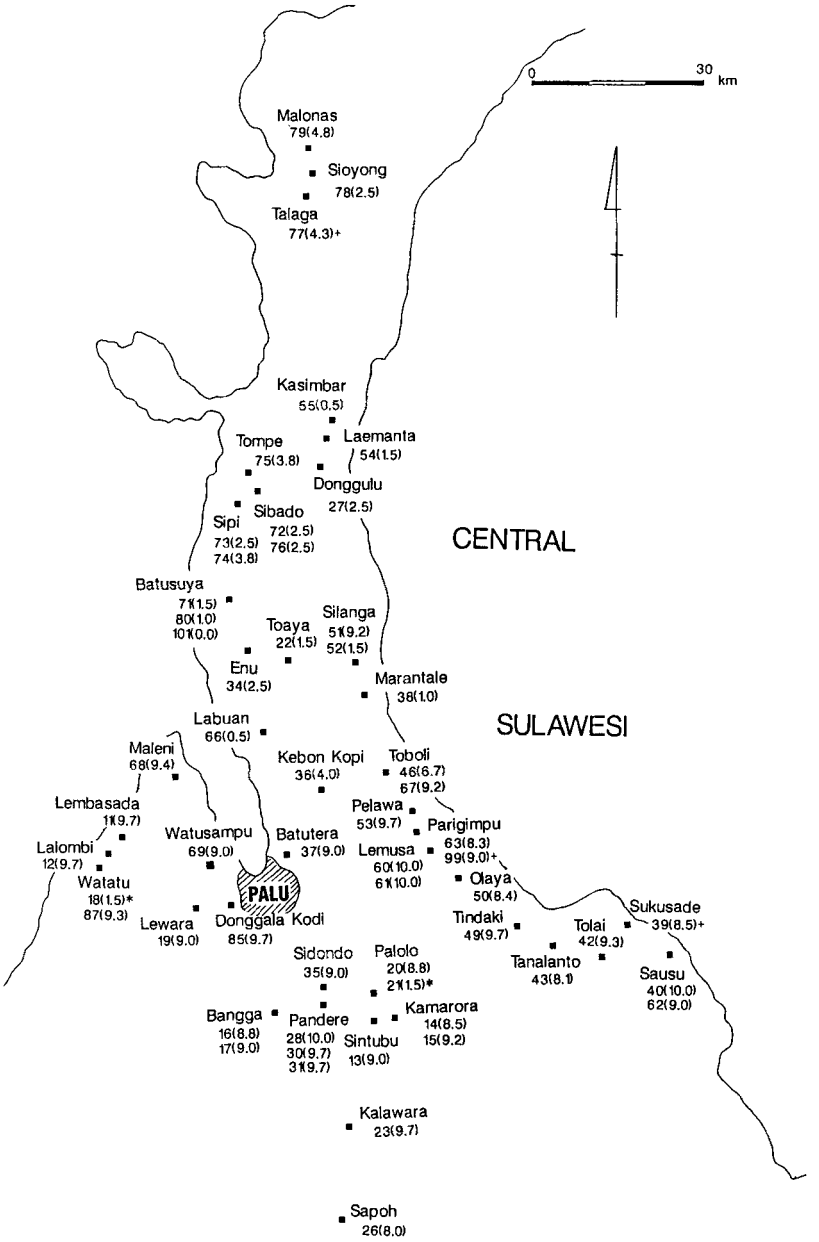

Fig. 1. Locations from which pet monkeys originated and the respective scores for the external characteristics of each monkey. The numerals indicate the codes for the various pet monkeys and the respective scores are shown in parentheses. Monkeys whose site of origin, as stated by the owner, could be judged to be the result of recent disturbance by humans or of possible misunderstanding after repeated transfer, are indicated by asterisks (see text). Scores indicated by a plus sign are those of monkeys for whom some external characteristics could not be fully appraised. In such cases, for *M. tonkeana*, full scores for the unappraised characteristics were added into the total (i.e. 1.0 for each characteristic), while no such scores were added in the case of *M. hecki*..

to our survey (information fidelity "D") and the stated origins can be inferred to be in error or to be the results of recent human disturbances, as mentioned above.

Two monkeys (*No. 36* from Kebon Kopi and *No. 46* from Toboli) revealed a mixture of the typical and intermediate external characteristics of both species. *No. 36*, a juvenile male captured at Gn. Ueriko about 1 km south of Kebon Kopi, displayed a combination of the identifying features of the two species: lighter brown hind-shanks (as *hecki*) and oval ischial callosities (as *tonkeana*). This monkey was also intermediate in terms of the characteristics of its ventral surface, crest of the rump patch, gluteal fields, and tail length (see Tables 1 & 2). The other monkey, *No. 46*, appeared to be similar to *M. tonkeana*, but its rump patch was very small and not very conspicuous. Furthermore, its tail was very tiny. These two monkeys were assigned scores of 4.0 and 6.7, respectively, and they were thus positioned between *tonkeana* and *hecki*. All of the other pet monkeys inspected had scores of more than 7.5 (*tonkeana*-type) or less than 2.5 (*hecki*-type), if infant or small juvenile monkeys were excluded. It is worthy of note that other monkeys examined originated from places near the borderland of these two species (i.e. *Nos. 22, 37, 38, 60, 61, 63,* and *67*) but possessed external characteristics typical of one species or the other. Thus, "hybrid" monkeys were found only in a very limited area, even though monkeys with all ten typical characteristics of either species were rather rare. The deviations can be recognized as individual differences.

One small juvenile (*No. 51*) was certainly *M. tonkeana* and was captured in the forest of Silanga, north of the borderland, where *M. hecki* (*Nos. 38* and *52*) is commonly found. We met the owner of *No. 51*, who had captured it in the nearby forest of Gn. Sumpe (information fidelity "A"). He testified that the monkey was caught when he pursued the mother inducing her to drop her son. Another *tonkeana* infant (*No. 67*) was said to have been captured in the northern forest of Toboli, while *No. 46* (a possible "hybrid") was captured in a slightly more southern area. If our information is correct, members of both species with rather "pure" external characteristics of either species (not intermediate forms) may be present together in that area.

Next, each external characteristic of both species was examined, and arranged by developmental stage (Table 2). All 102 pet monkeys were divided *a priori* into either *M. tonkeana* ($N=56$) or *M. hecki* ($N=46$). Monkeys *No. 36* and *No. 46* were included in *hecki* and *tonkeana*, respectively. Apparently, some external characteristics are very stable throughout the various developmental stages. In contrast, some other external characteristics are inadequate for assessing of the difference between the species because of the considerable variations that exist among individuals.

The color of the cheeks and rump patch of *hecki* exhibit no individual variation and is stable throughout all developmental stages. Similarly, the shape of the ischial callosities and the color of the forearms of *tonkeana* are stable in all monkeys inspected. The color of the ventral surface and the crest of the rump patch of *tonkeana* also varies only slightly. All the other external characteristics of the two species show individual variations to certain degrees. For example, the color of the ischial callosities of both species includes very wide individual variations, and it is impossible to discriminate between these two species solely on the basis of this criterion. The color of the cheeks of *tonkeana* also differs widely among individual monkeys. It is, however, quite clear that most of the ten external characteristics can indicate the difference between *tonkeana* and *hecki*, to some extent, and some external characters undergo gradual changes with the development of the monkeys.

The shape of the ischial callosities of *hecki* may alter rapidly from oval to reniform when the monkeys are still very young. The color of the hind-shanks of *hecki* also becomes lighter

Table 2. Developmental changes in each of ten external characteristics of *M. tonkeana* and *M. hecki*.

	M. tonkeana ($N=56$)					*M. hecki* ($N=46$)				
Color of cheeks										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0	2	7	3	1	1	8	11	9#	4	14
0.3		5	3	3						
0.7	1	3		2	4*					
1.0		1		3	16					
Color of ventral surface										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0							6	4	2	6
0.5		3				5	2	5#	2	8
1.0	4	12	6	9	20*	3	3			
Color of forearms										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0							4	3		7
0.5						1	3	4#	2	3
1.0	4	16	6	9	21*	7	4	2	2	4
Color of hind-shanks										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0						3	10	9#	4	13
0.3		1		1	2	4				1
0.7		3	1		8		1			
1.0	4	12	5	8	11*					
Rump patch: color										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0						8	11	9#	4	14
0.5		1	1	3	2*					
1.5	4	15	5	6	18					
Rump patch: crest										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0						7	10	7	4	12
0.5					3*	1	1	2#		2
1.0	4	16	6	9	17					
Gluteal fields										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0	1	1				6	10	7	4	14
0.5	1	2	3				1	2#		
1.0	2	13	3	9	21*					
Ischial callosity: shape										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0						1	7	8	4	14
0.5						1	4			
1.0	4	16	6	9	21*	6		1#		
Ischial callosity: color										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0		1			1*	1	5	3	4	7
0.5	3	1	2		1	3	5	6#		6
1.0	1	14	4	9	19	4	1			1
Tail length										
	Inf	Juv-s	Juv-l	SAd	Ad	Inf	Juv-s	Juv-l	SAd	Ad
0					1*	6	10	7	4	14
0.5		1		1	1	2	1	2#		
1.0	4	15	6	8	18					

Monkey *No. 36* is indicated by # in *M. hecki*, and monkey *No. 46* by * in *M. tonkeana*, respectively.

during the very early developmental stages. The color of the cheeks of *tonkeana* may gradually become white and the gluteal fields may become clearer as they develop. Similarly, the color of the ventral surface of *hecki* may become lighter and the color of their ischial callosities darken as the monkeys develop. The color of the forearms of *hecki* apparently becomes lighter as the monkeys develop, although it includes very wide individual variations. However, even after all these developmental changes have been considered, there are still wide individual variations in some of the external characteristics. Some of these variations may be the result of intervention by the owners. Black hair, in particular, may become somewhat brownish after repeated soaping, while white hair could become gray-yellowish after being dirtied.

Local variations in any of the external characteristic are not conspicuous because of the wide variations among individuals. Only the color of the forearms of *hecki* appears to exhibit some local variation. Among eight monkeys of *hecki* captured near the borderland with *tonkeana* (*Nos. 22, 34, 38, 52, 66, 71, 80,* and *101*) only three had darkish-brown forearms, while two scored 1.0 and three scored 0.5. Among the other seven monkeys (*Nos. 90, 91, 92, 93, 94, 96,* and *97*) captured far to the east of the area, near the borderland with another species, i.e. *M. nigrescens*, four had dark-brownish forearms and the other three, with somewhat intermediate coloring, were all small juveniles or infants.

Infant monkeys may possess more external characteristics in common during the very early developmental stages, irrespective of the differences between the species. Infants of both species have black hair over the entire body and oval ischial callosities. The rump patch of *tonkeana* and the light-brown color of the hind-shanks of *hecki* may not be so conspicuous, in part because of the paucity of hair. Thus, some of the diagnostic external characteristics appear progressively with age in these species.

The last week of the intensive survey was devoted to the observation of wild monkeys in the field, in the area where natural hybridization was suspected. The area near Kebon Kopi and Toboli is crossed by the trans-Sulawesi highway and observations were made while walking along the road. We encountered three or four groups of wild monkeys along the road winding through the mountains (56 to 59 km from Palu, in an area called Pancuran). Selected examples of our observations were as follows:

October 29, 1988, 57.7 km from Palu:
9:36 a.m. Two or three monkeys ran away after they noticed us. Some emitted sounds of alarm, while the other members of the group moved away, foraging on the ground. They often exchanged contact calls with each other.
9:48 a.m. Three adult monkeys were found on the ground. They all looked totally black with no white cheeks or brownish hind-shanks. Their rump patch was not conspicuous.
9:53 a.m. Some monkeys came together in the forest and moved to the west with frequent contact calls.
10:10 a.m. Two adults were seen. Both were black with no white cheeks and did not have a conspicuous rump patch. The hind-shanks of one monkey were somewhat brownish.

October 29, 1988, 56.5 km from Palu:
3:10 p.m. Four monkeys were found on the ground and they might have eaten some soil at the steep slope. All four of them were totally black without a conspicuous rump patch, white cheeks, or brown hind-shanks. The tails of two of them may have been the length and shape of those of *tonkeana* and not of *hecki*. Another adult male arrived. He had a smaller rump patch (extending approximately from his buttocks to the upper side of his knees). A juvenile monkey with a conspicuous rump patch was seen nearby.
3:23 p.m. An adult female (?) who was totally black with a very small rump patch and reniform ischial callosities passed by. Her hind-shanks were not brown.

3:30 p.m. A totally black adult with a very small rump patch and reniform ischial callosities passed by. Another adult with a whitish ventral surface then appeared. When he changed his position, his white rump patch could be seen clearly.
3:36 p.m. A totally black monkey went away and another with a small rump patch and reniform ischial callosities followed him.
3:47 p.m. Several monkeys climbed up a fig tree and picked the fruit. They were aware of the presence of the observer, who remained about 60 m away from them, but they did not flee from him.
4:02 p.m. An adult monkey which was totally black with a small rump patch, oval-shaped ischial callosities and gluteal fields, was seen eating figs.
4:04 p.m. The monkeys climbed down from the fig tree and became quiet. They appeared to be resting on the ground.

October 31, 1988, 56.9 km from Palu:
8:45 a.m. A group was detected from their vocal sounds. A monkey who was totally black with a small rump patch and slightly whiter cheeks was seen eating the fruit of a liana tree. Many monkeys exchanged vocal sounds both on the ground and in the trees.
8:59 a.m. An adult female with a small rump patch passed by emitting sounds. Just one monkey repeatedly emitted sounds while the others replied only occasionally.
9:03 a.m. A monkey began to emit alarm calls in the direction of the observers. Alarm calls were repeated for a while and several monkeys moved to the west.
9:24 a.m. A juvenile monkey which was totally black and had reniform ischial callosities passed by in the forest.

Similar observations were repeated during the course of the field observations. In general, the monkeys in the Pancuran area were totally black and lacked white whiskers. They tended to have a small, inconspicuous rump patch (or even none at all) and either type of ischial callosity. Although the conditions within the tropical rain forest and intense sunlight made it difficult for us to observe the external characteristics of the observed animals precisely, we are convinced that the monkeys in the area represent "hybrid groups" of *M. tonkeana* and *M. hecki*.

It is expected that many varieties of such "hybrids" may be visible along the road that passes through the forest of Kebon Kopi, Pancuran, and Toboli. It should be noted that, in Pancuran, we did not find any monkeys like *No. 36*, the pet from Kebon Kopi. Some animals observed about 35 km from Palu (near Kebon Kopi) on October 27 had browner hind-shanks but other parts of their bodies were blackish. Furthermore, one group observed about 50 km from Palu on October 15 included two monkeys: a black adult male with a large and conspicuous rump patch and oval ischial callosities, without white cheek-whiskers; and an adult with a very conspicuous rump patch, white cheek-whiskers and oval ischial callosities typical of *tonkeana*.

DISCUSSION

Complicated procedures may be necessary to establish unequivocally the presence of hybrid monkeys because we usually do not know the diagnostic features of such monkeys. However, when "peculiar" monkeys, with characteristics intermediate between those of two neighboring species, are found at the possible borderland, we can reasonably infer the presence of hybrids between the two species. Concerning the presence of "hybrid" monkeys between *M. tonkeana* and *M. hecki*, the observations of GROVES (1980) may be correct. GROVES (1980) also found an "intermediate" monkey, which originated from Kebon Kopi, but this monkey demonstrated a different combination of external characteristics

from our putative hybrids, as follows: reniform ischial callosities, large and pale rump patch, no gluteal field, darker arms and legs. He reported another "intermediate" monkey from Pandere (about 20 km south of Palu) with the following features: light cheeks; a pale, crested rump patch; gluteal fields; orange-colored, oval ischial callosities; striking brown hind-shanks; and brown forearms and ventral surface. Thus, when interbreeding between the two species occurs, many types of intermediate form can result. This conclusion is compatible with our field observations in the forest of Pancuran.

We did not find such intermediates near Pandere, but rather we observed only pure *tonkeana* monkeys (*Nos. 28, 30,* and *31*). Judging from the information obtained near Pandere, we infer that only *tonkeana* monkeys live in the forest there and no *hecki* monkeys are present in the area. The most plausible explanation for GROVES' report is that misleading information was given by the owner to GROVES or some artificial disturbances were responsible, as mentioned earlier. In fact, such artificial disturbances have become progressively more and more significant. One reason for these disturbances is the rapid increase in movement of the local people. Since the opening of the trans-Sulawesi highway in 1984, people in the area have been able to travel freely as far as Manado, the capital city of North Sulawesi Province, or to Ujung Pandang, the capital city of South Sulawesi Province. As a matter of course, they now travel around the area from their own homes very frequently. Furthermore, there are many settlements of immigrants from Java, Bali, and Lombok Islands. These immigrants may have family members or friends in different places and they often visit each other to discuss issues, to cooperate on agricultural projects, to earn money, etc. Most of the pet monkeys that were taken far from their original localities were captured originally by immigrants. The pet monkeys of *hecki* (*Nos. 18* and *21*) found within the range of *tonkeana* far south of the borderland were also kept by such immigrants.

The most important issue is where and how can the hybrid monkeys be produced, and to what extent. The occurrence of natural hybridization between *M. tonkeana* and *M. hecki* can no longer be denied. However, it may be limited to a very small area in the most proximal region of the northern peninsula and the area may not exceed 20 × 20 km (it is probably even smaller). Furthermore, the intergradation between these two species throughout a far wider area, as suggested by GROVES (1980), may be an artifact caused by a lack of adequate data. Due to a paucity of information, he was unable to analyze the developmental changes and inter-individual differences in each external characteristic. Many external characteristics in each species apparently reflect the state of development of the monkeys and do not represent clinal variations towards the two sides of the borderland. Recently, similar results to those of GROVES (1980) on the intergradation between these two species were reported by CIANI et al. (1989). However, the samples they collected in the area were even fewer in number than those inspected by GROVES (1980). Furthermore, the scoring of each external characteristic that might indicate hybridization between the species was not shown, and examinations of inter-individual differences in external characteristics were neglected. The developmental stage of the samples was also not indicated by CIANI et al. (1989). FOODEN's diagnostic external characteristics for each species of Sulawesi macaque (1969) are helpful for distinguishing species. However, as mentioned, each characteristic may involve some inter-individual differences and/or it may change with the development of the animals. Accordingly, intermediate scorings *per se* do not indicate hybridization between species. The diagnostic external characteristics must, in addition, be examined more carefully when the intergradation between species is considered. For example, *M. nigrescens* has large gluteal fields which extend upwards diagonally on the ischial callosities, even though FOODEN (1969) stated that they were rudimentary or absent (WATANABE, in prep.).

We will now consider how hybrids reproduce. The presence of small juveniles in the wild group at Pancuran may be indicative of the fertility of the hybrid monkeys. The reproductive fertility of hybrid monkeys has been confirmed for various combinations of the genus *Macaca* in the laboratory (e.g. BERNSTEIN & GORDON, 1980). Why, then, do these two species mostly preserve the differences in their external characteristics? The great majority of the *M. tonkeana* and *M. hecki* monkeys still possess well-defined external characteristics, by which we could easily allocate almost all of the pet monkeys examined to one or other of the species (when we add all the data obtained by our Japanese team, more than 200 *tonkeana* and *hecki* monkeys have been inspected to date). A "peculiar" monkey was also reported only from the area near Kebon Kopi (KAWAMOTO & SURYOBROTO, pers. comm.), and it is the only case of a possible hybrid found by the other members of our team.

The theoretical model of secondary intergradation (MAYR, 1963) may be applicable here. This model is relevant when two populations that were once isolated geographically come into contact again after they have diversified to some degree both genetically and morphologically. Such secondary intergradation may be characterized by a narrow zone of hybridization and steep morphological gradients in the area. FOODEN (1969) also described monkeys that were indicative of some intergradation from *tonkeana* to *hecki*. Out of three juvenile monkeys collected in 1916 at Labua Sore (about 25 km north of the present borderland), two had brownish hind-shanks with a blackish body, oval ischial callosities and somewhat intermediate forms of the crest of the rump patch. At present, no such monkey has been found and only typical *hecki* are seen in this area. These previous observations suggest, if the source of the collected specimens is correct, that the borderland of *tonkeana* and *hecki* has shifted about 25 km to the south within the past 70 years without expansion of the hybridization area. The present borderland is located within a rugged mountainous area, about 600 m above sea level or more. The lowest land (about 200 m above sea level) near the present borderland of *tonkeana* and *hecki* is located about 40 km to the north. The area might have become very narrow during the interglacial uplifts of sea level during the Pleistocene. However, the land is covered by tropical rain forests and the situation, supposedly, has not changed at least for the past several thousand years. Timbering operations, for example, began in the area only in 1978, and such a shift of the borderland must therefore have occurred before the recent large-scale disturbance by humans.

Natural hybridization between primate species has been reported in several cases. BERNSTEIN (1966, 1968) found two hybrid monkeys between *M. nemestrina* and *M. fascicularis* in a natural forest on the Malay peninsula. FOODEN (1964, 1971) also reported hybrids between *M. mulatta* and *M. fascicularis* at the borderland of these two species on the Indo-Chinese peninsula. However, these examples may have been restricted to small isolated forests where both species were confined as a result of recent disturbances by humans. The situation for *M. tonkeana* and *M. hecki* may be equivalent to that for *Papio anubis* and *P. hamadryas* observed by NAGEL (1973), SHOTAKE et al. (1977), and SUGAWARA (1979, 1982), although no conspicuous differences were recognized in the ecology and social behavior of the Sulawesi species. The hybrid monkeys between *P. anubis* and *P. hamadryas* may be produced solely by abductions of *anubis* females by *hamadryas* males, so that a narrow hybrid zone is formed at the borderland of these two species.

Concerning the problem of modern criteria for definition of a biological species, reproductive isolation should be considered in terms of gene flow (BIGELOW, 1965), not simply in terms of interbreeding. If hybrids have some deficiencies relative to individual monkeys of the parent species, selection will inhibit further increase in the numbers of hybrid monkeys and further gene flow between the two species. Consequently, two well-

integrated gene pools can be continuously maintained despite interbreeding. BIGELOW's concept appears to be the most productive when we consider the case of naturally occurring hybrids between *M. tonkeana* and *M. hecki*. We still do not have any detailed information on the ecology and behavior of the hybrids, which would help to advance the present discussion. Hybrid monkeys can also be seen at the borderland between *M. nigra* and *M. nigrescens* on the northern peninsula of Sulawesi (GROVES, 1980; WATANABE, in prep.). Furthermore, there is a possibility that interbreeding may occur between *M. nigrescens* and *M. hecki* in the borderland between them (WATANABE, pers. obs.). The degree of intergradation should be different and depend on the species from which the hybrid monkeys are produced. The clinal differences in the Sulawesi macaques from the more specialized northern species, *M. nigra* and *M. nigrescens*, to the more generalized southern species, *M. maura* and *M. tonkeana* (ALBRECHT, 1978; FOODEN, 1969; HILL, 1974), undoubtedly reflect the repeated periods of isolation and contact of fairly divergent populations. Isolation tends to promote endemic divergences among Sulawesi macaques and contact may allow the species to exchange genes to a certain extent. Only further studies can elusidate the degrees of diversification of the Sulawesi macaques and related evolutionary processes as a whole.

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REFERENCES

ALBRECHT, G. H., 1978. *The Craniofacial Morphology of the Sulawesi Macaques: Multivariate Approaches to Biological Problems.* Contributions to Primatology, Vol. 13, S. Karger, Basel.

BERNSTEIN, I. S., 1966. Naturally occurring primate hybrid. *Science*, 154: 1559–1560.

————, 1968. Social status of two hybrids in a wild troop of *Macaca irus*. *Folia Primatol.*, 8: 121–131.

———— & T. P. GORDON, 1980. Mixed taxa introductions, hybrids and macaques systematics. In: *The Macaques: Studies in Ecology, Behavior and Evolution*, D. G. LINDBURG (ed.), Van Nostrand Reinhold, New York, pp. 125–147.

BIGELOW, R. S., 1965. Hybrid zones and reproductive isolation. *Evolution*, 19: 449–454.

CIANI, C. A., R. STANYON, W. SCHEFFRAHN, & B. SAMPURNO, 1989. Evidence of gene flow between Sulawesi macaques. *Amer. J. Primatol.*, 17: 257–270.

FOODEN, J., 1964. Rhesus and crab-eating macaques: intergradation in Thailand. *Science*, 143: 363–365.

————, 1969. *Taxonomy and Evolution of the Monkeys of Celebes (Primates: Cercopithecidae).* Bibliotheca Primatologica, No. 10, S. Karger, Basel.

————, 1971. Report on primates collected in western Thailand, January–April 1967. *Fieldiana Zool.*, 59: 1–62.

GROVES, C. P., 1980. Speciation in *Macaca*: the view from Sulawesi. In: *The Macaques: Studies in Ecology, Behavior and Evolution*, D. G. LINDBURG (ed.), Van Nostrand Reinhold, New York, pp. 84–124.

HAMADA, Y., T. WATANABE, O. TAKENAKA, B. SURYOBROTO, & Y. KAWAMOTO, 1988. Morphological studies on the Sulawesi macaques. I: Phyletic analysis of body color. *Primates*, 29: 65–88.

HILL, W. C. O., 1974. *Primates: Comparative Anatomy and Taxonomy. VII. Cercopithecinae*; Cercocebus, Macaca, Cynopithecus. Wiley, New York.

KAWAMOTO, Y., Y. HAMADA, B. SURYOBROTO, T. WATANABE, M. IWAMOTO, & O. TAKENAKA, 1987. A case study on the genetic variation within and between troops of the black ape, *Macaca nigra*. *Kyoto Univ. Overseas Res. Rep. Stud. Asian Non-human Prim.*, 6: 15–17.

————, O. TAKENAKA, & E. BROTOISWORO, 1982. Preliminary report on genetic variations within and between species of Sulawesi macaques. *Kyoto Univ. Overseas Res. Rep. Stud. Asian Non-human Prim.*, 2: 23–37.

————, ————, B. SURYOBROTO, & E. BROTOISWORO, 1985. Genetic differentiation of Sulawesi macaques. *Kyoto Univ. Overseas Res. Rep. Stud. Asian Non-human Prim.*, 4: 41–61.

MAYR, E., 1963. *Animal Species and Evolution*. Belknap Press of Harvard Univ. Press, Cambridge.

NAGEL, U., 1973. A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatol.*, 19: 104–165.

SHOTAKE, T., K. NOZAWA, & Y. TANABE, 1977. Blood protein variations in baboons: I. Gene exchange and genetic distance between *Papio anubis, Papio hamadryas* and their hybrid. *Japan J. Genet.*, 52: 223–237.

SUGAWARA, K., 1979. Sociological study of a wild group of hybrid baboons between *Papio anubis* and *P. hamadryas* in the Awash Valley, Ethiopia. *Primates*, 20: 21–56.

————, 1982. Sociological comparison between two wild groups of anubis-hamadryas hybrid baboons. *Afr. Stud. Monog.*, 2: 73–131.

TAKENAKA, O., M. HOTTA, Y. KAWAMOTO, B. SURYOBROTO, & E. BROTOISWORO, 1987a. Origin and evolution of the Sulawesi macaques, 2: Complete amino acid sequences of seven β chains of three molecular types. *Primates*, 28: 99–109.

————, ————, A. TAKENAKA, Y. KAWAMOTO, B. SURYOBROTO, & E. BROTOISWORO, 1987b. Origin and evolution of the Sulawesi macaques. 1: Electrophoretic analysis of hemoglobins. *Primates*, 28: 87–98.

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