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NOTES ON THE SYSTEMATICS OF *BABYROUSA* (ARTIODACTYLA, SUIDAE)

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With 4 plates

SUMMARY

Skins and skulls of *Babyrousa babyrussa* have been studied; the species is divisible into three living subspecies: *B. b. babyrussa* (syn. *frosti*) from Buru and Sula, *B. b. togeanensis* from Malenge, and *B. b. celebensis* from the northern arm of Celebes. A skull from near Kulawi, central Celebes, tends towards *babyrussa*, and may represent a surviving population of the inadequately characterised *B. b. bolabatuensis*, known as a subfossil from the southern arm of Celebes. Teeth of the latter form decreased in size through time. The possibility of the species having been introduced into Buru and Sula is discussed.

INTRODUCTION

The remarkable babirusa (genus *Babirousa* Perry, 1811) attracted early notice in western scientific circles, despite its restricted distribution (see Mohr, 1958 for a brief pre-Linnaean history). It commanded attention because of the bizarre appearance of the male, not only for Europeans but also, perhaps, for Indonesians (see below). Modern zoology has confirmed that it is indeed no "ordinary pig", as shown by the anatomical study of Davis (1940): alone among the Suidae it retains four terminal tendons to M. plantaris; the arrangement of tendons to M. extensor digitorum communis resembles the peccaries; M. coracobrachialis has two heads, as is usual in ruminants; the stomach is complex, and the origin of M. omohyoideus again resembles the peccaries (Saban, 1968). While Deninger's (1909) claim that it had descended from a Miocene anthracothere can surely no longer be maintained, Thenius (1970) could see no common ancestor with the other Suidae more recent than the Oligocene, justifying its allocation to a separate subfamily, Babyrousinae.

History of taxonomy

After a period when it was variously misassigned to Borneo, Sumatra, Amboina and other places (as noted by Sody, 1949) its occurrence in Celebes and Buru was finally confirmed, and authors set about elucidating its variation from place to place. First, Deninger (1909), on the basis of remarkably large samples for that period (16 from Buru, 10 from Celebes) distinguished the Celebes babirusa — taking Buru as type locality of *B. babyrussa* — as a separate species, *Babirusa* (sic) *celebensis*. The distinguishing characters of the Celebes species were the wrinkled, nearly hairless skin, contrasting markedly to the well-haired skin of the Buru species; the longer, narrower skull; the upper toothrow longer, above 73 mm, the nasals constricted between the canines of the males, and the longer, thicker upper canines with their alveoli upright instead of forwardly inclined. As a consequence of the difference in initial direction of the upper canines, in side view they are not overlapped by the backcurving lower canines as they are in the Buru form.

Later Dammerman (1929), comparing "a rather large series" (about seven?) of skulls from Buru with four from Celebes, found the following differences: the Buru skulls are shorter and broader, their profile less straight; the frontals have deep sharp-edged furrows, instead of shallower with rounded edges as in Celebes specimens; and the supraorbital foramen is more or less concealed from dorsal view. However, in only one of the four Celebes skulls were the nasals greatly constricted. The upper canines in the Buru skulls are parallel to each other, or diverge, whereas in two of the Celebes skulls they converge and nearly touch in the middle of their curve. Some of these characters, he notes, are similar to those which distinguish domesticated from wild pigs. Dammerman was aware of Deninger's paper but had "no access" to it.

As a matter of fact Lesson (1827), although referring to Buru, had in effect described Celebes babirusas under the name *Babirussa alfurus*; but Deninger, as well as Thomas (1920), Sody (1949), Laurie & Hill (1954) and others, showed that Lesson merely intended to rename Linnaeus's *Sus babyrussa* (even quoting the type locality as Buru) to avoid tautonymy.

Thomas (1920) reported on eleven skulls from Taliabu, in the Sula islands, comparing them with the Buru form after first noting that in Deninger's canine and nasal characters they followed the Buru, not the Celebes pattern. Retaining the division into two species, he described the Sula form as *B. b. frosti*, differing from *B. b. babyrussa* in its slightly smaller size, conspicuously smaller canines, narrower bullae, and more slender paroccipital processes. However, it is unclear how many skulls from Buru were available

for comparison, only one being mentioned (this one, however, being the one figured by Seba and so the chief basis for Linnaeus's description, is the lectotype of the species): judging by the registration numbers, only one other Buru skull would seem to have been in the British Museum at that time.

Sody (1949) compared 10 skulls from Celebes, 4 from Malenge (Togean islands), 8 from Buru, and 4 from Sanana (Sula Islands). These last he referred to *frosti* with a query, as "judging on the description, there seem to exist differences" from the type series from Taliabu. He went on to describe the Malenge specimens (including 3 skins and one head-skin) as a new race, *B. b. togeanensis*. The new race was described as hairy like *babyrussa* (and also *frosti*, a fact not known to Thomas), with the underparts, as far as the sides of the upper lip and insides of the limbs, much lighter than the rest of the body. The toothrow was said to be much shorter than in *celebensis* but rather longer then in *frosti*, though about the same as in *babyrussa*; M^3 was narrower than in *celebensis*, perhaps a little smaller than in the other two; the nasals, pinched in like in *celebensis*. By implication, Sody included the Celebes form, too, in the single species *B. babyrussa*.

One further subspecific name has been applied to a babirusa. In 1964, F. de Beaufort, in a catalogue of type specimens of ungulates in the Paris museum, drew attention to a mounted babirusa skin from an animal brought back alive by Quoy and Gaimard and stated in the museum catalogue to be from Celebes. However, in the collector's manuscript catalogue the specimen is listed as from "Moluques". This, according to De Beaufort, makes the specimen a novelty, as the babirusa appears not to have been recorded from there since then; so it would have formed a geographic variety (now perhaps extinct), to be called *Babyrousa babyrussa Merkusi* (sic), after M. Merkus, governor of the Moluccas, who presented the animal to Quoy and Gaimard. Everything about this name is inexplicable; the Moluccas, then as now, included Buru, type locality of the species; the specimen was already in captivity in Merkus' residence, and could as easily have been presented to him from Celebes as from anywhere else; the capitalisation of the trinomial; and surely it was pointless to create a nomen nudum, which even if it represents a valid form will be displaced by any name (with description appended) which someone in the future cares to award.

Mohr (1958) reviewed the subspecies described up to that time, and presented photos of living *celebensis* and *frosti*, showing clearly the naked wrinkled skin of the former and the hairy covering of the latter. The snout of *frosti* is, as she notes, markedly more pointed than that of *celebensis*, and would seem to be more mobile in life. Other interesting photos include one of a female skull — perhaps the first published photo of the skull of

the rather unspectacular, tuskless female — and one (Abb. 18) of a *frosti* skull said to be female, with small tusks in the upper jaw, and canines larger than usual for a female in the lower jaw. The specimen, evidently a young adult, is a wild-shot one, collected by Rosenberg; without supporting evidence, I would incline to consider it a male with rather short tusks, especially considering its evident youth.

Two extinct forms, one recent and one fossil, have been described by Hooijer (1948; 1950). Three M_3, one M^2 and one M^3 from Beru and Sompoh, near Cabenge in Sulawesi Selatan (South Celebes), associated with the Pleistocene giant suid *Celebochoerus heekereni*, were very much larger than most living homologues (than all, in the case of the M^2 and the two complete M_3), and were described as a subspecies *Babyrousa babyrussa beruensis* (Hooijer, 1948). Numerous teeth from the Holocene cave deposits at Bola Batu, also on the southern peninsula, were assigned to the subspecies *Babyrousa babyrussa bolabatuesis* by Hooijer (1950), as having "Teeth... of less average size (than Celebes specimens), comparable to that found in *Babyrousa babyrussa babyrussa* (L) of Boeroe and in *Babyrousa babyrussa frosti* (Thomas) of the Sula Is.". In other words, the new subspecies was distinguished from the other Celebes race but not from the Buru and Sula ones. But as the Bola Batu deposits seem fairly recent (they contain apparent dog remains, and 16th century Chinese sherds), the implication certainly is that if babirusa had survived on the southern peninsula up to the present they would be, in dental characters at least, more like *babirusa* than *celebensis*.

The present study

A study of babirusa taxonomy was begun in July 1975 at the Zoological Museum, Bogor, as a by-product of a study of southeast Asian Suidae. Further material was studied in various European museums in November and December 1976 and February 1977, and finally again in Bogor in July 1978. Standard measurements were taken on skulls and teeth, skin characters were recorded, and special attention was paid to those characters described in the literature (above) as diagnostic of one form or another. Dr. G. G. Musser kindly sent measurements and descriptions of specimens in the American Museum of Natural History (New York), and these have also been utilised in the present study.

Skin

The Bogor Museum (MZB) and American Museum of Natural History (AMNH) have good collections of babirusa skins; other museums little or none. Altogether I could study personally 3 (4?) from Celebes, 3 from

Malenge, 5 from the Sula Is. (of which 4 were from Sanana), 2 (3?) from Buru, and the type of *merkusi*. In addition, I received descriptions of 9 skins from Celebes and 6 from Malenge in the AMNH.

All Buru and Sula skins have conspicuous long thick hair all over the head, body and legs. Of the 4 Sanana MZB specimens, 3293, a male, has hair that is mostly creamy gold with just a few black hairs intermingled, mostly towards the foreparts, and a dorsal stripe of unmixed golden hairs; but the rump hairs, in a triangle with its apex in the lumbar region, are entirely black, with the golden dorsal stripe continuing through it. The head is like the body, but round each eye is a ring of black and the hairs on the back of the ears are black. The cheeks and limbs are pale. MZB 3291, a female, is similar, but the hairs are sparser. MZB 3292, a female, has long dense hair of the same colour, but with no black hairs at all except a few sparse ones on the rump, round the eyes, and on the back of the ears. MZB 2014, a juvenile female, on the other hand has the fairly dense long hairs entirely black all over the body. Finally, a skin in the Amsterdam Museum, ZMA unreg., from "Sula Islands", has much sparser hair, especially on the hind parts, mainly white but with some black on the snout.

Of the Buru skins one (MZB 1871), a female, resembles MZB 3293 from Sanana, but has black hairs on the rump only and a few round the eyes. The other, ZMA unreg., female, has pale fawn hairs all over, rather sparser than the Bogor skin. Another skin, ZMA 9122, a juvenile said by Mohr (1958: 57) to be from Buru, but with "Celebes" on the present label, has thick black hairs all over.

All these skins, therefore, have a conspicuous hair-cover with both a light (fawn or gold) and a dark (black) hair type, varying in predominance, but tending to be differently distributed over the body. All skins, if complete in that region, show a well-developed tail tuft. The two unregistered ZMA skins (one from Sula, one from Buru) are noticeable paler on the underparts, a feature said by Sody to distinguish the Togean race.

The three *togeanensis* skins in Bogor, as Sody states, are variable in colour: mostly fawn, but some hairs in all skins are black, generally with fawn tips; they are paler fawn in the mid-dorsal region and black on the forehead, while the underparts are pale. The six AMNH Togean skins vary from "brown" to (in one case) black, which sounds in part similar to the Bogor skins and implies the same range of variation as in Buru and Sula. As in the latter, there is always a well-developed tail tuft. A difference, however — apparently the only consistent difference — is that the hairs, though still conspicuous, are much less long and dense.

The three Celebes skins in Bogor — two from Bumbulan, one from

G. Ile-Ile in the same region — are markedly different: the hair very sparse and short, dark brown but lighter in the median dorsal region; the overall effect is of complete nudity. Of the nine skins, all from Bumbulan, in the AMNH collection, Musser (pers. comm.) describes 5 as "sparse", 2 as "medium dense", 2 "dense" and either black or "brown", and in the substantial breeding group in the Surabaya zoo, evidently from Celebes, some animals are indeed much more conspicuously hairy than others. A skin in Amsterdam, ZMA 9121, from Celebes, also has a conspicuous hairy coat. Guillemard (1886: 205) describes a male from Lembeh island, off Bitung in Minahasa, as being "covered with a very fine yellowish down", and he also notes the colour polymorphism.

If there is less difference in hairy convering between the Celebes babirusa and the rest than has commonly been described, one substantial difference does remain: the small size and sparsity of the tail tuft, in which all specimens from Celebes — AMNH material included — differ consistently from all those from other islands.

Skull: a. non-metrical comparisons

Dammerman (1929) found that the dorsal profiles of his Buru series were less straight than those from Celebes. In the present study, two-thirds of the skulls from both Buru and Celebes have a profile that is noticeably concave at the nasal root (as have 40% from Taliabu and all from Malenge). This distinction therefore cannot be maintained.

The difference in degree of expression of the frontal furrows is much more diagnostic. The furrows are not sharp-edged in any skull from Minahasa or Malenge, nor in 16 out of 18 from the Bumbulan region, but they are in 12 out of 16 from the Sula Is. and in 23 out of 29 from Buru. Both males and females show this difference; in Buru and Sula they seem to become sharper-edged with maturity. The associated feature of the supraorbital foramen (which lies at the posterior end of the furrows) being overhung, concealed from dorsal view, in Buru but not in Celebes skulls, is not quite as good: it is visible from above in 16 out of 17 from Minahasa, 17 out of 18 from Bumbulan, and in all of 8 from Malenge, but also in 6 out of 15 from Sula and 17 out of 32 from Buru.

The canines of males differ markedly between the various geographical groups. As Deninger (1909) found, they tend to be much longer and thicker in Celebes than in Buru; Sula skulls align with Buru, and this time the Malenge skulls also tend to align with Buru. However, a Buru skull (Leiden, cat. ost. b) has the largest canines of any seen in this study. A difference that seems to differentiate in every case between males from northern Celebes

and from Sula or Buru is the forward-rotated alveolus of the maxillary canine in the latter, such that, as Mohr (1958) stressed, the upper canine in Sula and Buru emerges much more closely behind the lower, and in side view the lower canine crosses lateral to the upper (pl. 1 fig. a, b). In Celebes male skulls the upper canine emerges vertically and the lower is always distinctly anterior of it (pl. 3 fig. a). In Malenge skulls the canine alveoli are rotated as in Buru, but less markedly in most cases (pl. 2 fig. b).

As Dammerman (1929) noted, the maxillary canines usually diverge or run parallel to each other in Buru skulls; they do slightly converge, however, in 10 out of 26 skulls, and even cross in one (Leiden, cat. ost. b). In Sula, somewhat by contrast, they converge in 9 out of 13, but in the restricted series from Taliabu they converge in 8 out of 10. They converge in all Malenge skulls, and in all but three of 22 skulls from northern Celebes (they cross in one of these).

The differences described by Thomas (1920) to distinguish *frosti* (Taliabu) from *babyrussa* (Buru) are not very convincing. The skulls do average slightly narrower, but not significantly. The canines are small in both as a general rule: it merely happens that in the lectotype of *babyrussa* they are rather large. Mohr (1958: 65) figures a Sula skull with unusually large canines. The bullae and paroccipital processes are not different.

Hooijer (1950) noted that, although most babirusa skulls lack P^2 or DM^2, this tooth is present on at least one side in 7 out of 13 skulls from Sula, compared to one out of 17 from Buru and two out of 15 from Celebes. Of the specimens not seen by Hooijer, one (MZB 2015) out of 14 from Buru has a P^2, making a full total of 2 out of 31, or 6.5%; 2 out of 4 from Sanana, making a full total of 9 out of 17, or 53% for Sula as a whole; none from Malenge; and one out of 9 from Celebes, giving a total of 3 out of 24, or 12.5%. Thus it is confirmed that the frequency of this anomaly is much higher in the Sula islands than elsewhere.

Skull: b. Metrical comparisons

A number of standard measurements were taken on skulls and teeth of all babirusa specimens studied, as well as two (distances between upper canines: (1) at their roots, (2) in the middle of their length) designed to bring out the convergent/divergent contrast. The results, population by population, are given for males in Table 1.

The two samples from the northern peninsula of Celebes, Minahasa and Bumbulan (the latter includes in addition one specimen each from Monano and Muton) are very alike metrically, as they are non-metrically. Bumbulan skulls are broader across the zygomata and canine roots and have a longer

TABLE I

Skull measurements of geographical samples of male *Babyrousa*

(a) Groups

	Minahasa			Bumbulan			Malenge			Taliabu			Buru		
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d
Total length	16	293.9	9.90	13	296.9	14.78	5	309.0	6.75	10	280.2	11.91	26	281.8	1 .86
Condylobasal	16	277.0	13.25	13	280.1	11.03	5	285.2	4.44	8	271.8	10.08	22	266.8	9.59
Bizygomatic	17	126.4	6.93	13	133.3	6.58	5	129.0	3.74	10	121.7	6.20	26	127.5	3.72
Palate l.	17	181.2	8.97	12	184.5	8.06	5	185.4	3.85	10	181.3	7.86	26	180.1	6.58
Toothrow l.	9	75.3	1.66	9	80.3	4.06	6	71.7	1.75	1	68.0	-	6	69.0	1.67
Occipital br.	8	70.6	9.90	13	67.7	7.16	5	68.4	3.85	10	64.3	3.86	26	69.5	4.53
Occipital ht.	7	66.6	5.02	13	66.0	4.03	5	62.8	3.96	9	57.8	5.33	24	61.	4.57
Canine roots	9	57.8	1.92	12	62.3	6.43	6	61.0	2.35	10	50.1	2.69	26	56.1	4.02
Canine middle	6	24.7	11.52	10	15.4	16.30	5	0.0	0.00	10	27.8	20.25	18	53.7	23.09
M^3 length	7	24.4	1.60	13	25.4	1.98	6	20.8	0.75	10	22.1	1.10	15	22.6	1.50

(b) Single specimens

	Lembeh	Moa	Sanana
Total length	288	252	265
Condylobasal l.	(271)	(242)	254
Bizygomatic br.	134	128	121
Palate l.	183	(155)	169
Toqthrow l.	(76)	69	67
Occipital br.	80	54	64
Occipital ht.	(73)	(46)	56
Canine roots	61	51	47
Canine middle	12	15	64
M^3 length	23	23.9	21

toothrow, but not one of the differences exceeds the traditional subspecific limits, with the coefficient of difference (C.D., i.e. difference between the means divided by sum of the standard deviations) greater than 1.28. The single specimen (Cambridge Zoology Museum, 13.002) from Lembeh, an island off the eastern coast of Minahasa, divided from it by a channel about half a kilometre wide, falls within two standard deviations of the Minahasa sample for all measurements; Deninger (1909) gives measurements, many of them comparable, for three more skulls from Lembeh, one of them (Dresden 2476) the type of *celebensis*.

The Malenge skulls average larger than those from Minahasa or Bumbulan, and have a shorter toothrow and shorter M^3, lower occiput, and the distance across the middle of the upper canines (a metrical expression of their invariable convergence) is zero. The third molar difference is beyond the traditional subspecific level of distinction from both the Minahasa (1.53) and Bumbulan (1.68) samples as is the toothrow length from the Bumbulan (1.48), though not from the Minahasa (1.06) sample. Taken in conjunction with the external differences, the Malenge form should be allotted to a different subspecies from the northern peninsula form.

The Taliabu skulls are smaller in almost every measurement than are the Celebes ones. The toothrow length and breadth across canine roots are significantly smaller than in the two mainland samples, and the latter and total skull length differ significantly from the Malenge material (C.D. above 1.28). Taken, again, in conjunction with the external differences, this confirms that the Taliabu form should be recognised as a subspecies distinct from the Celebes mainland and Malenge forms.

The single adult male skull from Sanana, the old name for the island of Sulabesi southeast of Taliabu in the Sula group, is smaller than all but one of the Taliabu skulls, but does not fall beyond the two standard deviation limits in any of its measurements.

Buru skulls are again small; they differ significantly from the Celebes mainland and Malenge samples in the smaller total length and condylobasal length, from the mainland samples also in the smaller toothrow length. But they do not differ significantly in any measurement from the Taliabu sample; and as it will be recalled that there are no external or visual skull differences either, there are no grounds for maintaining a subspecific distinction.

The female skulls are few in number. Thomas (1920) quotes Frost, the collector of the Taliabu sample, to the effect that the males defend the females so courageously that females are hard to kill. The female samples (Table 2) differ from one another in just the same manner as do the males, with the sole exception of the Malenge skulls, which are not larger than the Celebes mainland ones, unlike the corresponding males. Females are otherwise some 30 mm shorter in total and condylobasal length than are the respective males.

A most interesting specimen is the (slightly damaged) skull of a male from G. Malema, 1200 m, Moa, Kulawi district, central Celebes (MZB 12115, pl. 3 fig. a). The skull was purchased in 1977 from villages by WWF and PPA representatives, and is the first known specimen from Celebes that is not from the northern peninsula, although Dr. G. G. Musser (pers. comm.) saw live specimens several times in the same general area. The skull is

TABLE 2

Cranial and dental measurements of female *Babyrousa*

	Minahasa	Bumbulan		Malenge	Sanana	Buru	
	n = 1	n = 5		n = 2	n = 2	n = 3	
		mean	s.d.			mean	s.d.
Total length	257	262.6	5.22	257.5	246.5	253.0	11.36
Condylobasal	249	250.2	8.47	244.0	238.5	243.7	14.01
Bizygomatic	122	117.0	3.24	113.5	110.0	118.7	9.61
Palate l.	169	160.4	7.57	156.0	155.0	164.0	11.14
Toothrow l.	-	81.0	5.34	69.5	70.0	67.0 (1)	-
Occipital br.	70	52.4	5.18	50.5	54.0	60.7	7.09
Occipital ht.	55	50.8	5.31	47.5	48.5	52.3	3.21
Canine roots	52	-	-	36 (1)	35.0	40.7	4.73
P^3 length	-	11.0	0.71	10.5	10.5	9.0 (2)	-
P^4 l.	-	10.5	0.58 (4)	9.5	9.0	9.3	1.15
M^1 l.	-	13.8	0.84	13.0	12.5	11.5 (2)	-
M^2 l.	17.0	18.0	1.22	16.5	17.0	16.0	1.00
M^3 l.	-	23.8	1.79	21.0	21.0	20.3	0.58
P_3 l.	-	12.4	1.34	12.0	11.0 (1)	10.5	0.50
P_4 l.	-	12.4	1.14	12.0	10.5	11.0	0.00
M_1 l.	-	14.4	0.89	13.25	12.5	12.3	0.58
M_2 l.	-	17.0	0.71	15.75	16.0	15.7	1.04
M_3 l.	-	26.6	1.82	22.0	23.5	22.7	1.53

remarkably small — its total length being 11 mm less than the next smallest male skull — but it is fully adult. Total length is about four standard deviations from the Minahasa sample, three from Bumbulan, eight from Malenge, 2.4 from Taliabu and 2.3 from Buru. Toothrow length is more than two standard deviations from Celebes and 1.5 from Malenge; and canine roots more than two from the Malenge and Minahasa samples, but not quite (1.76) from Bumbulan. Occipital breadth is nearly two standard deviations, usually more, from all other samples.

The canines in the Moa skull are short, and in the upper jaw the alveoli are rotated forward to about the same degree as in some of the Malenge skulls. The frontal furrows are shallow with rounded edges, and the supra-orbital foramen is visible from above, as is usual in Celebes and Malenge

skulls; and the upper canines meet in the middle. There is no trace of P^2. From a general survey of its features, therefore, the Moa skull resembles a tiny version of a Malenge skull.

A simple way of comparing samples within a species is the Penrose multivariate statistic. This has the advantage that it can be calculated without the need for a computer, and that unlike the widely used Mahalanobis D^2 the size component of the distance is separated out and does not distort the final result, which should depend on shape alone. On the other hand it does not take allometry into account. It can be used, in any case, as a general guide to overall shape resemblances.

Table 3 shows the results of a Penrose statistic (on males only), calculated using a programme written for a Sharpe desk calculator by Dr R. V. S. Wright, of Sydney University. In Table 3(a) are the distances between the groups: size above the diagonals, shape below. The size statistics merely say what one already knew: Taliabu skulls (and those from Buru to a lesser extent) are very small compared to the rest. In the shape distances, Taliabu and Buru skulls are very close, Bumbulan and Minahasa are fairly close;

TABLE 3

Penrose size and shape statistics for *Babyrousa* skulls

(a) Groups

		Minahasa	Bumbulan	Malenge	Taliabu	Buru	
Minahasa		x	-0.10	0.03	0.69	0.12	SIZE
Bumbulan	SHAPE	0.30	x	0.25	1.32	0.45	
Malenge		0.65	0.81	x	0.44	0.03	
Taliabu		0.34	0.91	0.86	x	-0.23	
Buru		0.41	0.93	0.96	0.19	x	

(b) Single specimens

	SIZE			SHAPE		
	Lembeh	Moa	Sanana	Lembeh	Moa	Sanana
Minahasa	-0.08	1.90	1.19	0.57	1.50	0.96
Bumbulan	0.00	2.89	1.99	0.77	1.18	1.71
Malenge	-0.22	1.44	0.83	0.98	2.56	1.91
Taliabu	-1.28	0.29	0.07	1.19	1.22	0.33
Buru	-0.42	1.06	0.55	0.87	1.15	0.27

and these two pairs are closer to one another than either is to Malenge — a somewhat curious result. Three single specimens can now be brought in and compared to the groups. The Lembeh skull is, predictably, nearest to those from Minahasa in shape, and identical to Bumbulan in size. The Sanana skull is very close in size to Taliabu, and in shape even slightly closer to Buru. The Moa skull, though not far from Taliabu in overall size, is not like any other in shape.

Dentition

Table 4 gives the means and standard deviations for cheekteeth in different samples, both living and fossil. The samples for the living are based on males only; comparison with Table 2 shows that most of the cheekteeth in females are about the same size, only third molars being much smaller.

Applying the coefficient of difference test to the modern samples, the only cases where the values rise above 1.28 are M^3 for the Malenge sample in comparison with both Bumbalan and Minahasa — which was discovered previously — and M_3 for the Malenge/Bumbulan comparison, but only just. Compared to M^1 (Table 4(c)) the Taliabu and Buru samples have small P^3 but unreduced P^4, while M^3 is rather large in the North Celebes samples and very small in Malenge. Tooth sizes do differ between samples, but not at a level that bears on their taxonomic differentiation.

Mention has already been made that Hooijer's (1950) subfossil South Celebes subspecies *bolabatuensis* was distinguished from the living Celebes form but not from the Buru and Sula ones. In Table 4(b), the means and standard deviations, calculated from Hooijer's raw data, are presented. As Hooijer noted, the figures are in most cases very close to those for Buru and Sula, with the noteworthy exception of the first molars, both upper and lower, which are disproportionately large compared especially to the other molars. The means also seem close to the Moa skull, without such marked disproportion. Whether this can be interpreted to mean that the Moa individual represents a living population of *bolabatuensis* must await the discovery of more complete material of the latter.

Of the other fossil samples, Batu Ejaya teeth are mostly smaller than Bola Batu, as are some of those from the upper level (A-B) of Panganreang Tudea, though by a much smaller amount: it may be doubted whether, if larger samples were available, these latter would be any different at all from Bola Batu. On the other hand, the teeth from the lower levels (C-D) of Panganreang Tudea are uniformly larger than Bola Batu, and compare well with those from Minahasa.

Batu Ejaya has a C^{14} date reported as 920 ± 275 B.P. (Mulvaney &

TABLE 4

Dental measurements (n; X; s.d.) of recent and fossil *Babyrousa* (Anteroposterior diameters only)

(a) Living

	Minahasa			Bumbulan			Malenge			Taliabu			Buru			Lembeh	Moa
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	mean	s.d.
p^3	6	10.67	1.21	12	11.00	1.18	6	10.67	0.82	10	9.90	0.74	14	9.71	0.70	9.0	10.6
P^4	6	9.75	0.76	12	10.20	0.58	6	10.00	0.63	10	9.50	0.71	15	9.90	0.60	9.0	10.2
M^1	3	13.30	0.58	12	13.25	0.78	6	12.83	0.41	9	12.89	0.60	14	12.32	1.03	11.0	13.4
M^2	9	17.22	0.97	13	17.65	1.07	6	16.33	0.52	10	16.70	0.82	23	16.80	0.67	16.0	17.1
M^3	7	24.36	1.60	13	25.40	1.98	6	20.83	0.75	10	22.10	1.10	15	22.60	1.50	23.0	23.9
P_3	7	11.43	0.53	13	11.90	1.23	6	11.83	0.98	10	10.20	0.79	16	10.60	0.73	11.0	13.5
P_4	7	11.70	0.76	13	11.70	0.83	6	12.00	0.63	10	11.20	0.63	16	11.50	0.52	11.0	12.6
M_1	7	13.71	0.49	13	14.40	0.96	6	12.83	0.75	9	12.78	0.67	15	12.70	0.88	13.0	14.1
M_2	7	16.30	0.49	13	16.90	0.86	6	15.67	0.52	10	26.30	0.67	15	16.60	0.61	16.0	15.5
M_3	7	25.40	1.62	13	27.20	2.31	6	23.50	0.55	10	24.70	0.82	15	24.50	0.99	24.0	23.1

(b) Fossil and subfossil

	Bola Batu			Lompoa		Panganreang Tudea				Batu Ejaya		Beru & Sompoh	
						C - D		A - B					
p^3	22	9.95	0.51			1	10.5	2	9.60				
P^4	27	9.64	0.37			1	10.0	3	9.90	0.35			
M^1	27	13.33	0.52	1	13.4	1	13.6	1	13.4		1	12.8		
M^2	37	16.69	0.72	1	16.4	2	17.6	2	16.5		2	16.25	1	20.2
M^3	43	22.32	1.24			1	23.8	3	21.73	0.96	1	19.8	1	25.4
P_3	9	10.48	0.45											
P_4	12	11.55	0.48			1	11.9	1	10.9					
M_1	9	13.37	0.52					3	13.70	0.72				
M_2	15	16.27	0.81	1	16.8			1	16.8		1	17.8		
M_3	15	23.80	1.11					2	23.20				2	29.35

(c) Ratio of Maxillay Tooth Lengths to length of M^1

	Minahasa	Bumbulan	Malenge	Taliabu	Buru	Lembeh	Moa	Bolabatu
p^3	.80	.83	.83	.77	.79	.82	.79	.75
P^4	.73	.77	.78	.74	.80	.82	.76	.72
M^2	1.29	1.33	1.27	1.30	1.36	1.46	1.28	1.25
M^3	1.83	1.92	1.62	1.72	1.83	2.09	1.78	1.67

Soejono, 1970), that is to say around A.D. 1030. In that Bola Batu has what are said to be dog remains (Hooijer, 1950), it may also be fairly late; but on the analogy of Timor (Glover, 1970) this could mean as much as 4000 B.P. Mulvaney & Soejono (1970) cast doubt on the reality of the claimed sequence at Panganreang Tudea, at least as far as the artefact associations are concerned, and mention Van Heekeren's opinion that the potsherds from there are intrusive. There are also no domestic or introduced animal remains at Panganreang Tudea, unlike Batu Ejaya. The implied sequence, Panganreang Tudea — Bola Batu — Batu Ejaya, is consistent with the hypothesis of a gradual dental size reduction in this species as in so many others in southeast Asia during the early Holocene (Hooijer, 1950).

The Pleistocene babirusa from the same region (Beru and Sompoh), *Babyrousa babyrussa beruensis* Hooijer, 1948, was noticeably larger in dental dimensions than any modern form. This makes the size-reduction hypothesis all the more plausible.

Subspecies and synonyms

The following subspecific classification of the species is proposed:

Babyrousa babyrussa babyrussa (Linnaeus, 1758)

Sus babyrussa Linnaeus, 1758. "Borneo"; recte: Buru.
Aper orientalis Brisson, 1762. Name unavailable.
Babyrousa quadricornis Perry, 1811.
Babirussa alfurus Lesson, 1827. Buru.
Babirussa babyrussa frosti Thomas, 1920. Taliabu, Sula Islands.

Material studied from: — Sula Islands: Pulau Sulabesi, ca. 2.03 S, 125.59 E; Pulau Taliabu, 1.50 S, 124.40 E. Buru: S. Yalua, ca. 3.45 S, 126.50 E; Wa Kruma, NW. Buru; Lijotiking; Yuai Hi, NW. Buru; Lake Wakallo; Wai Hi. Localities mentioned in literature: Gunung Kapala Madang, 3.15 S, 126.15 E; Gunung Katina, ca. 3.21 S, 126.25 E; Wai-Hotton; Upper River Bilkofan, ca. 3.22 S, 126.25 E (Deninger, 1909). Upper (River) Wa Ha, ca. 3.22 S, 126.26 E; Kayeli, 3.25 S, 127.07 E; Wa'Kuma, SW. Buru; Wai Hi, NW. Buru (Dammerman, 1929).

Distribution: — Buru; Sula Islands (at least the islands of Taliabu and Sulabesi).

Characters: — Body hair always long and thick; tail tuft well-developed. Skull with frontal furrows mostly deep, sharp-edged. Upper canines of males usually short, slender, with alveolus forwardly rotated, so that lower canine crosses upper in lateral view; generally divergent or parallel to each other, or weekly convergent. Size small, with small teeth. Skulls from the Sula Islands have more convergent upper canines in the male than those from Buru, and more commonly retain P^2 (pl. 1 fig. a, b; pl. 2 fig. a).

Babyrousa babyrussa togeanensis Sody, 1949

Babirussa babyrussa togeanensis Sody, 1949. Malenge, Togean Islands.

Material studied from: — Pulau Malenge.

Distribution: — Known only from Malenge.

Characters: — Body hair less long and dense than in the previous subspecies, paler on underparts; tail tuft well-developed. Skull with frontal furrows always shallow, with sloping edges. Upper canines of males usually short, slender, somewhat rotated forward, always converging. The largest race, but teeth small, especially the third molars (pl. 2 fig. b).

Babyrousa babyrussa celebensis (Deninger, 1909)

Babirusa Celebensis Deninger, 1909. Pulau Lembeh, N. Celebes.
Babyrousa babyrussa Merkusi De Beaufort, 1964. Nomen nudum. "Les Moluques"; probably northern Celebes.

Material studied from: — Minahasa: Manado, 1.32 N, 124.55 E; Lumpias, 1.35 N, 124.59 E; Saludaa, 0.20 N, 123.27 E; Likupang, 1.40 N, 125.05 E; Kema, 1.23 N, 125.05 E; Pulau Lembeh, 1.25 N, 125.17 E. Bumbulan: Bumbulan, 0.31 N, 122.04 E; Gorontalo, 0.33 N, 123.05 E; Monano, 0.54 N, 122.42 E; Gunung Ile-Ile, 0.55 N, 121.45 E; Sumalata, 0.59 N, 122.31 E; Muton, 0.27 N, 121.13 E.

Distribution: — Northern peninsula of Celebes, at least as far west as Bumbulan, and including the offshore island of Lembeh.

Characters: — Body hair generally short and sparse; tail tuft small and sparse. Skull with frontal furrows mostly shallow, with sloping edges. Upper canines of males generally long and thick, the alveoli vertically implanted, so that upper canine emerges vertically and is not crossed by lower in lateral view; converging in almost all cases. Size fairly large. Skulls from the Bumbulan region are somewhat broader than those from Minahasa and have larger teeth (pl. 3 fig. a).

Babyrousa babyrussa beruensis Hooijer, 1948

Babyrousa babyrussa beruensis Hooijer, 1948. Beru, near Cabenge, S. Celebes; Pleistocene.

Distribution: — Known from Pleistocene deposits at Beru and Sompoh.

Characters: — Teeth as far as known noticeably larger than in any living form.

Incertae sedis:

Babyrousa babyrussa bolabatuensis Hooijer, 1950

Babyrousa babyrussa bolabatuensis Hooijer, 1950 Bola Batu caves near Watampone, early (?) Holocene.

Characters: — Known parts not certainly distinguishable from *B. b. babyrussa*, except perhaps by reduced size of first molars; but presumably distinct.

Skull from Gunung Malema, Moa, near Kulawi, central Celebes: — Size very small, with especially narrow occipital crest; otherwise mainly a diminutive version of *B. b. togeanensis*, though dental proportions like *bolabatuensis*. It is conceivable that this skull could represent a living population of *bolabatuensis* (pl. 3 fig. b).

Discussion

The impoverished and unbalanced nature of the mammalian fauna of Buru led Dammerman (1929) to suggest that all mammals except the bats had probably been introduced by human agency, including the babirusa. The anatomical characters which he attributes to the Buru babirusa in distinguishing it from the Celebes form are, however, insubstantial, so that his claims that it has characters of domestication cannot be maintained. His statement that there is no Buruese name for the species would also seem to be in error, as Stresemann (1925) gives the names 'donit' (Maserete) and 'gonit' (Lisela), although in the Lumara dialect it is called simply 'bodi' (= white). Interestingly, Deninger (1909) says that the general name is the Malay/Indonesian 'babi putih' (= white pig), while in Masarete it is known in the local dialect as 'bodi'. Whether this can be taken to mean that in the interval between the visits of Deninger and Stresemann a simple descriptive term in Masarete had given place to a genuine name introduced from elsewhere can perhaps be solved by field work in that region among the older residents.

But Dammerman's hypothesis that the babirusa, along with other mammals, is a human introduction in Buru, seems plausible enough. At any rate, its near identity with the Sula Islands form indicates that it has spread very recently from the one to the other. It is even possible that it is not indigenous to the Sula Islands either, for it appears not to exist on Peleng, an island well-known from the collections of the Archbold Expeditions, and an essential stepping-stone from Celebes to the Sula group had babirusa extended their range without human help. The lack of material from east-central Celebes makes it impossible to confirm or refute this hypothesis at the moment, but it is worth noting that the subspecies *togeanensis* is intermediate between *celebensis* and *babyrussa*, while the Moa skull is a further step towards the Buru/Sula form.

Nor are linguistic studies much help here. The languages of the Sula group are entirely unknown (W. A. Foley, pers. comm.), while the names given by Mohr (1958) for various Celebes languages are all quite different

from the enigmatic Buruese 'donit'/'gonit'. Adriani's dictionary of Bare'e (a language centred on the Poso district) gives the same words as Mohr, variants of the stem word 'rari', also 'boibi' for the young.

Certainly the babirusa attracted widespread attention among both Indonesians and Europeans. Even if, with Mohr (1958: 67-68), we reject the notion that it was known to the Romans in the 1st century A.D., its first European description, by Piso in 1658 (Mohr, 1958: 52) is still remarkably early. It was kept and even bred by petty rulers in Celebes as a potential diplomatic gift (Dammerman, 1929: 154).

It is even plausible that it was incorporated into Balinese art. The 'Raksasa' — a demon, half-human, half-animal — is represented with a curly tusk emerging from either cheek (pl. 4 fig. a, b), a notion which seems rather difficult to account for unless the artists had a tradition of an animal which does actually have this disposition (Anthony Forge, pers. comm.). Bali was included in the Bugis (S. Celebes) trade network in the 18th (?) century (Tobing, 1977: 44) and there was a Buginese colony there in 1817 (Boon, 1977: 25); one of the tangible results of such trade will have been the introduction of Bali cattle into South Celebes, where they remain to this day the only domestic breed.

Conclusions

The original distribution of the babirusa is difficult to reconstruct, but it seems likely that it was originally confined to Celebes (including the Togean Is.). It is less ecologically resilient than the anoa, for example, and has vanished from the extensively cultivated southern peninsula of Celebes; on the other hand, its range has evidently been extended by human agency to Buru; its apparent absence from Peleng suggests that it may be intrusive also in the Sula group. As a skull from central Celebes approaches the Buru and Sula subspecies, the origin of the latter may perhaps be sought here. Further specimens are needed to solve this problem, but as the babirusa is a rare animal, they should not be obtained not by traditional "collecting" but by purchasing, or soliciting as gifts, trophy skulls kept in local villages, which is how the Moa skull was obtained.

Whether the hypothesis of its introduction into Buru and Sula is valid or not, the babirusa has quite evidently long been regarded as an extraordinary beast, adopted into Balinese art as the acme of animality, and made known in Europe at an unexpectedly early date.

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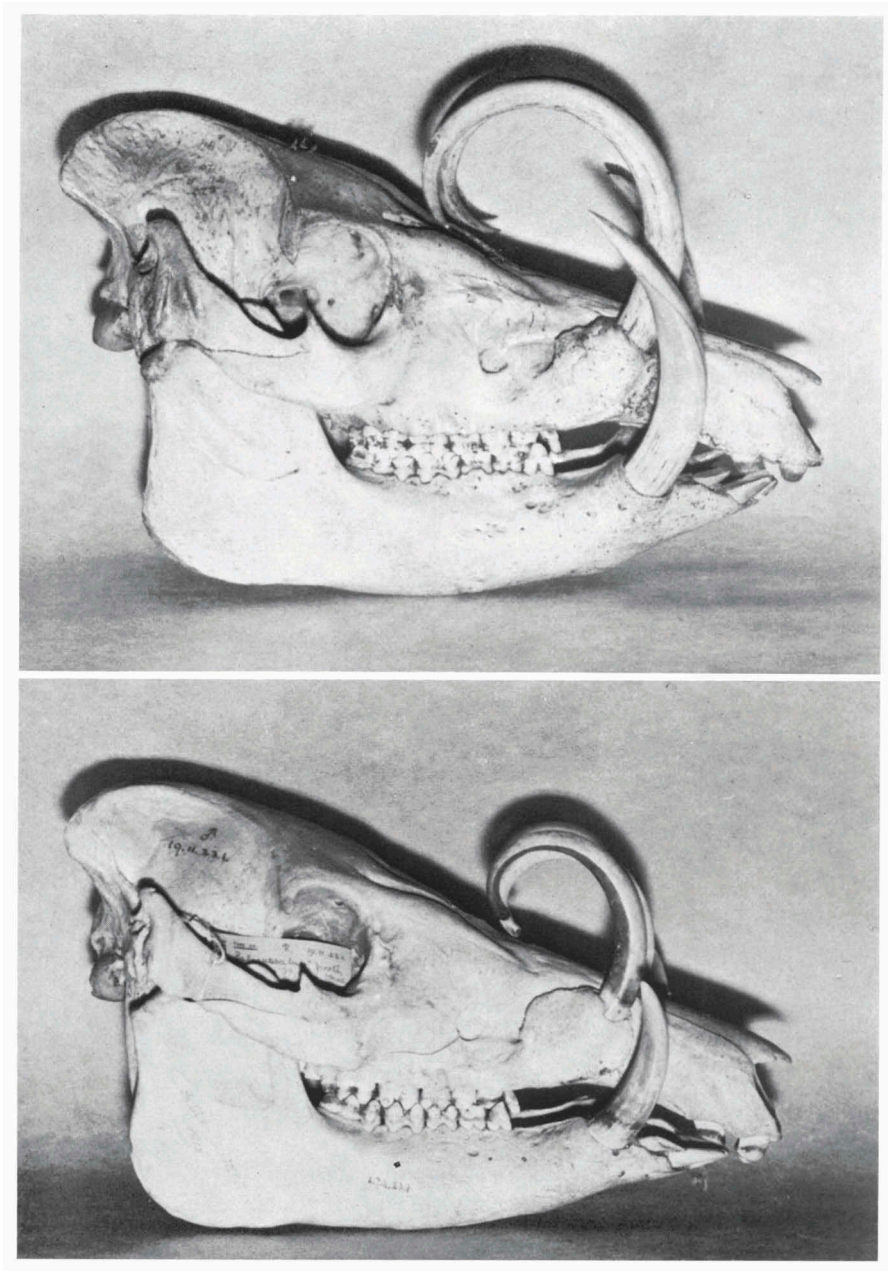

Fig. a (upper). BM (NH) 67.4.12.223, ad. ♂, Buru. Lectotype of *Sus babyrussa* Linnaeus, 1758. Formerly in the Seba collection. Fig. b (lower). BM (NH) 19.11.23.1, ad. ♂, Pulau Taliabu, Sula Islands. Holotype of *Babirousa babyrussa frosti* Thomas, 1920.

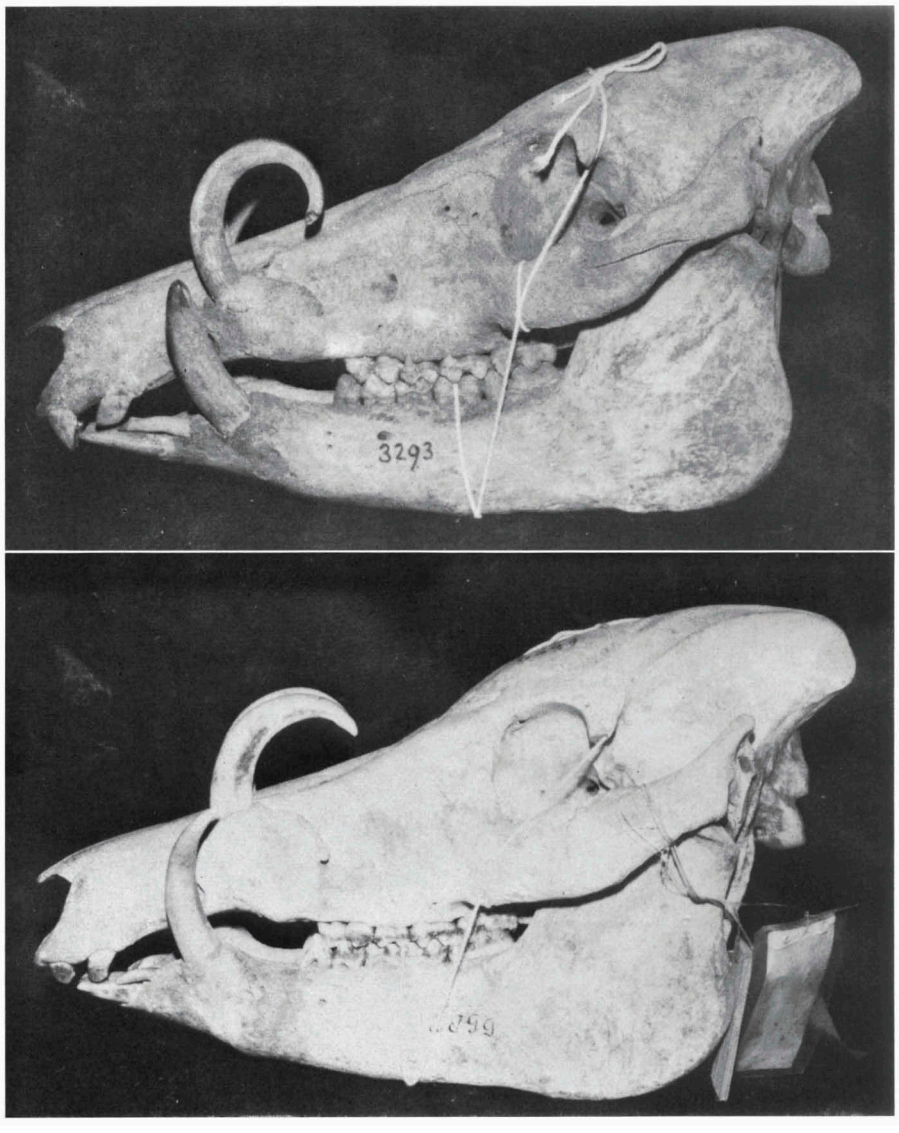

Fig. a. (upper). MZB 3293, young ad. ♂, Sanana, Pulau Sulabesi, Sula Islands. Fig. b (lower). MZB 6899, young ad. ♂, Pulau Malenge, Togian Islands. Holotype of *Babirousa babyrussa togeanensis* Sody, 1949.

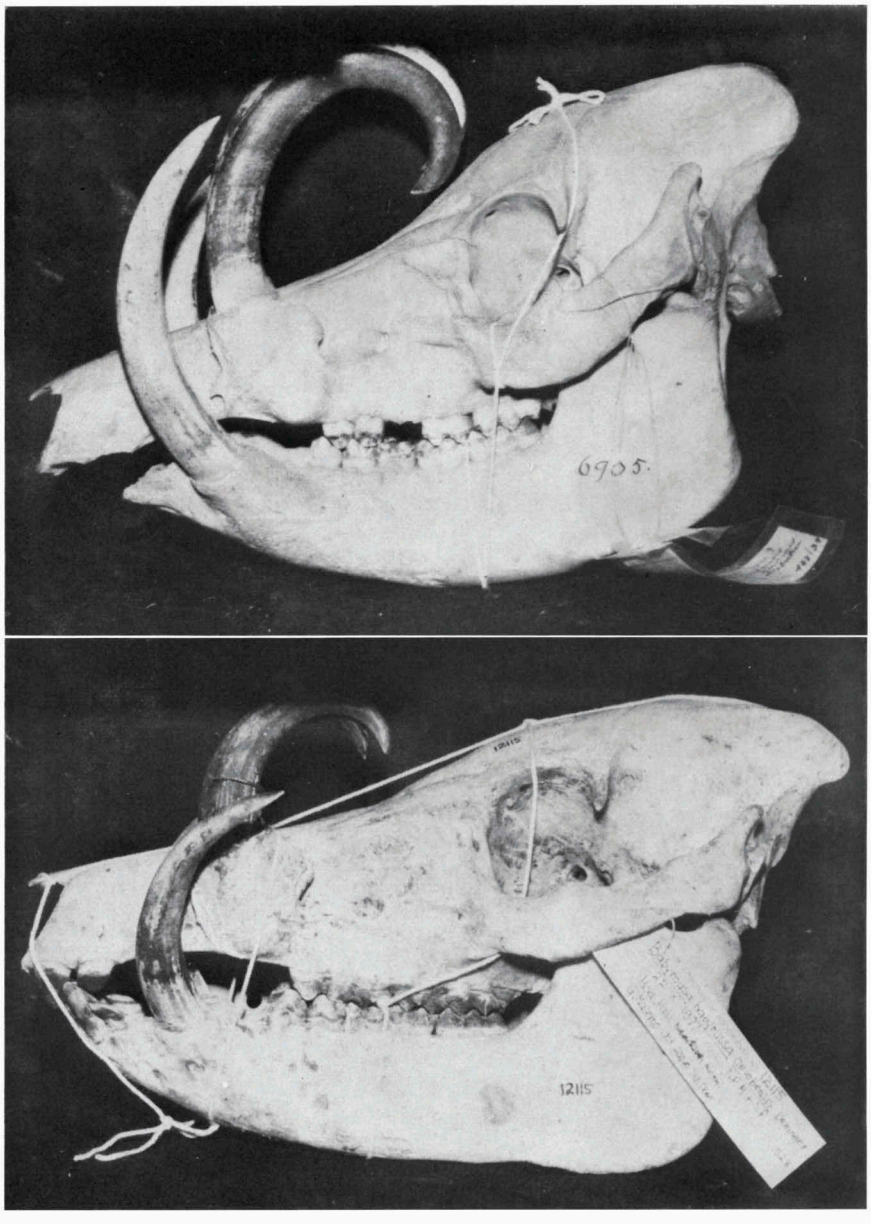

Fig. a (upper). MZB 6905, ad. ♂, Manado, Kab. Minahasa, N. Celebes. Fig. b (lower). MZB 12115, ad. ♂, Moa, Gunung Malema, 1200 m, Kulawi, central Celebes.

Fig. a (left). Head of a noble Raksasa, member of the kingdom of Lanka in the Ramayana epic. Fig. b (right). Pemurtian form of a god; assumed by gods when enraged, this form has many arms and nine Raksasa-type heads, differing only in the presence of a third eye in each. Both from a traditional painting from Karangasem, E. Bali, probably early 20th century. Courtesy, Prof. Anthony Forge.