



Taxonomy of wild pigs (*Sus*) of the Philippines

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Native wild pigs of the Philippines are now in grave danger of extinction. Study of available material indicates that three species are present: Sundaland *Sus barbatus* on Palawan, and two endemic species, *Sus philippensis* (with three subspecies, one of them here described as new) on Luzon, Mindanao, Basilan, Leyte, Samar, Catanduanes and Mindoro, and *Sus cebifrons* on Negros, Cebu and Panay. Specimens from Jolo, Masbate and Bohol presently remain unallocated to species, and may reflect the occurrence of hybridization.

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ADDITIONAL KEY WORDS: *Sus philippensis* *Sus cebifrons* Philippine pigs.

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INTRODUCTION

The taxonomic history of the Philippines wild pigs has been a checkered one. They have in the main been regarded as conspecific with taxa from outside the archipelago. The Luzon pig, the first taxon to be described, was referred to *Sus*

celebensis, a species hitherto known from Sulawesi in Indonesia (Nehring, 1989; Sanborn, 1952); the taxon from Negros was assigned to the same species (Sanborn, 1952); that from Mindanao was referred to *Sus verrucosus* of Java (Forsyth Major, 1897; Sanborn, 1952); the pigs from Palawan and from Balabac were regarded as forms of Bornean *Sus barbatus*. (Nehring, 1894; Forsyth Major, 1897); and the whole lot has been placed in *Sus barbatus* (Groves, 1981; Mudar, 1986), and all except the Palawan and Balabac forms in *Sus verrucosus* (Mohr, 1960). Most recently, it has been proposed provisionally to separate the Philippines taxa from all others as two independent species (Groves & Grubb, 1993; Oliver *et al.*, 1993).

The reasons for aligning Philippine pigs with *S. barbatus*, rather than with *S. celebensis* as was done by Sanborn (1952) and Mohr (1960), were their relatively great facial elongation, the shape of the preorbital fossa, the small size of the male's canine apophysis, the longitudinal convexity of the nasals, the lower-crowned skull, and the presence of cheek whiskers.

Recently new cytogenetic findings on Philippine wild pigs have been made available (de Haan *et al.*, 1993). These add a further dimension to the taxonomic question.

The wild pigs of many, but not all, of the major islands of the archipelago have received special names, as follows:

Balabac: *balabacensis* Forsyth Major, 1897

Palawan: *ahoenobarbus* Huet, 1888; *palavensis* Nehring, 1889

Calamianes: *calamianensis* Heude, 1892

Luzon: *philippensis* Nehring, 1886; *marchei* Huet, 1888; *effrenus*, *frenatus*, *minutus* and *microtis* Heude, 1892

Mindanao: *mindanensis* Forsyth Major, 1897

Cebu: *cebifrons* Heude, 1888

Negros: *negrinus* Sanborn, 1952

In addition, Heude (1892) named several other taxa from the Philippines, and figured their teeth, but gave no further information on either their distinguishing characters or their localities (though some of the localities can be deduced from their names): *Sus jalaensis*, *arietinus*, *megalodontus*, *crassidens*, *mamilensis* and *inconstans*.

There is now a conservation crisis in the Philippines; forest clearance and excessive hunting has depleted many species, especially large mammals, to population fragments. In the present case, wild pigs are in danger of being eliminated by genetic contamination from domestic pigs, if not of being hunted out (Oliver *et al.*, 1993). There is an urgent need to reassess the taxonomic status of the different island populations, in order to identify conservation priorities; at least one taxon, *cebifrons*, is regarded as endangered, and genetic contamination from domestic pigs is suspected as a risk factor in all cases (W.R. Oliver, pers. comm.). Groves's (1981) revision was of necessity cursory where Philippines forms were concerned, and larger samples were recently sought in the U.S. collections. The results of this new study, based on better material, are described here.

MATERIAL AND METHODS

Material

Specimens were studied in October of 1994 in the following collections: Smithsonian Institution (U.S. National Museum), Washington, D.C.; Field Museum of Natural History, Chicago; and Michigan State University Museum (kindly loaned to the Field Museum on my behalf). In July 1996 the Heude collection, long considered lost, was 'rediscovered' in the Beijing Institute of Zoology, and specimens were studied and measured as far as time permitted. In July 1991, a recently acquired collection was studied in the Natural History Museum, London. These are in addition to specimens previously studied in the Natural History Museum (London), the Muséum National d'Histoire Naturelle (Paris), and the Zoologisches Museum (Berlin), and by Dr Peter Grubb on my behalf in the American Museum of Natural History (New York) and elsewhere, and reported on in Groves (1981). Measurements of other skulls were kindly supplied by Dr Larry Heaney and Dr Alastair Macdonald. A full specimen list is given in the Appendix. Numerous photographs of living specimens of known origin, not all of them reproduced here, were consulted. These were kindly supplied by Messrs William Oliver, Roger Cox, Roland Scitre, Roland Wirth, L. R. Heaney, Michael Koll and Ms Lori Tan.

Basic methodology

Some of the measurements taken were the same as those listed in Groves (1981: 67). Other measurements were as follows:

- Greatest depth of zygomatic process of zygomatic arch
- Mesiodistal length of upper canine of females
- Diameter of inferior surface of lower canine of males
- Diameter of posterior surface of ditto
- Lower toothrow length from canine to third molar
- Lengths of each premolar and molar, upper and lower jaws
- Maximum widths, molars and P4, upper and lower jaws
- Lengths of the following diastemata:
 - Upper canine to first premolar
 - Lower canine to first premolar
 - First to second lower premolar

Most of the skulls were photographed from above, below and behind, as were the upper and toothrows. Skulls and teeth were compared visually both at the time of study and from the photographs afterwards.

Skins were extensively annotated.

Skull and tooth measurements were compared by calculating simple statistics (means, standard deviations), on bivariate graphs, and by multivariate analysis.

Multivariate analysis

Multivariate analyses were done using the Discriminant program of SPSS-Windows, on a desk computer (PC) at the Australian National University. The skull measurements used were:

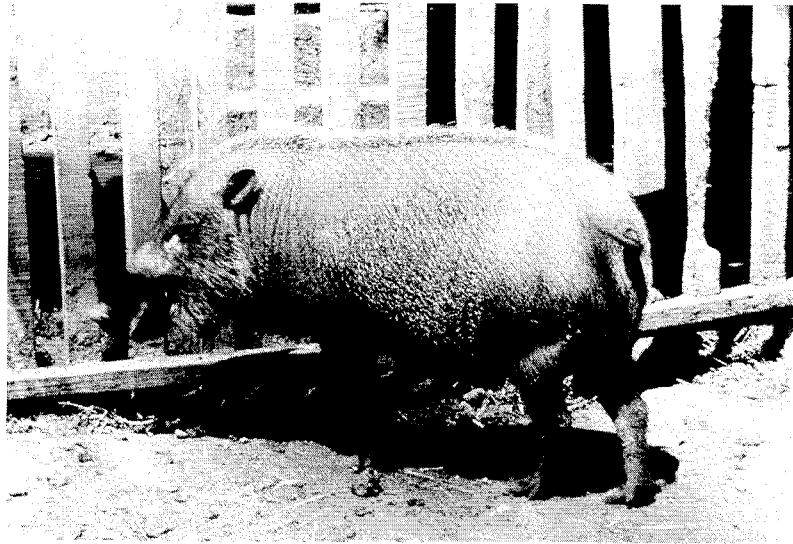


Figure 1. *Sus barbatus ahoenobarbus*, adult female, from Coron Island, Calamianes. Ecosystems Research and Development Bureau (ERDB/DENR), Los Baños (photo W. Oliver).

Greatest skull length
 Condylbasal length
 Bizygomatic breadth
 Occipital (crest) breadth
 Occipital height
 Nasal length
 Palate length
 Incisor row length

The tooth measurements were the lengths of both maxillary and mandibular premolars and molars, and the widths of P₄ and the molars; the lengths of maxillary incisor row, molar row, and total premolar-molar row; the length of the mandibular canine-premolar-molar row; and the lengths of the mandibular diastemata. Maxillary and mandibular dental variables were entered into separate analyses. Only males were used, given constraints on sample sizes. The number of skulls used in these analyses was: Palawan, 7; Mindoro, 3; Luzon, 9; Mindanao, 7; Negros, 6; *Sus celebensis*, 4; two skulls, one each from Leyte and Jolo, were entered as unknowns.

The number of toothrows was: Palawan (including Balabac) - maxillary 2, mandibular 2; Mindoro - 3, 2; Luzon - 16, 5; Mindanao - 13, 8; Negros - 4, 3; Jolo - 3, 2; *Sus celebensis* - 2; a maxillary specimen from Leyte and two mandibular specimens from Masbate were entered as unknowns.

Cladistic analysis

Finally, 30 characters were coded in Philippine and other *Sus* taxa (*Sus barbatus*, *S. verrucosus*, *S. celebensis*, *S. scrofa*) and a cladistic analysis was run using PAUP 3.0b (Swofford). Outgroup was *Potamochoerus*. Character states, ordered by presumed

polarity, are listed in Table 6; note that, because of the caveats concerning the polarity of male mandibular canine shape expressed by Van der Made & Moya-Sola (1989) and Van der Made & Han (1994), for canine shape the outgroup was coded 1 and scrofic and verrucosic canines were coded 0 and 2-3 respectively.

RESULTS

Skin and external characters

Clear and consistent inter-island differences in pelage and other external characters emerged from examination of skins and photos from each locality, as follows:

Palawan, Calamianes

A female from Palawan at the Ninoy Aquino Nature Centre and a female from Coron, Calamianes, at the Ecosystems Research and Development Bureau (ERDB/DENR), Los Baños (Fig. 1), have short, sparse grey to whitish hair with reddish-toned grey skin showing through; short white upstanding spinal stripe, somewhat longer on nape and crown than on back; muzzle black, and rest of face white, the hairs elongated along the sides of the face, becoming longest on the jaw angles. The disk is at right angles to the plane of the muzzle. A male, in rather poor condition, in Malabon Zoo in Quezon City is dark red-brown in colour, both the very short (strongly abraded) hair and the skin; no mane or crown tuft, but the body hair stands upright along the spine; curly grey-white hair covers the dorsum of the snout from eyes to canine apophyses. The skin has transverse costal ridging right round the thorax, presumably related to its poor state of health. The face is slightly concave between the eyes; the snout is convex. The snout disk points noticeably downwards. These all resemble closely the external appearance of *Sus barbatus*, the Bearded Pig of Borneo (see descriptions in Mohr, 1960; Groves, 1981).

Luzon

A living adult female held at ERDB/DENR at Los Baños has sparse black flank hairs, with the red-brown skin showing through; the face is more densely black-haired with no white snout band but brightly white tufts on the jaw angles; the crown tuft is short, black, and continued as a short black nuchal mane. Another captive female, held at ERDB at Laguna Bay, differs in that the hairs of the crown tuft are longer and mainly white.

BM 97.8.4.1, an old male, has bristly black hair on the head (there is no body-skin) with no face-band; there are gonial whorls overlying very slight warts; preocular warts are quite large. A living male in the ERDB/DENR collection at Los Baños is black, with a thick, forward-leaning toupée which is black with a few white-tipped hairs anteriorly; the face has a few whitish hairs intermixed; the preocular warts are large; the gonial warts are prominent, elongated obliquely along the jawline, and furnished along their extent with long white bristles. A living 10-year-old male from

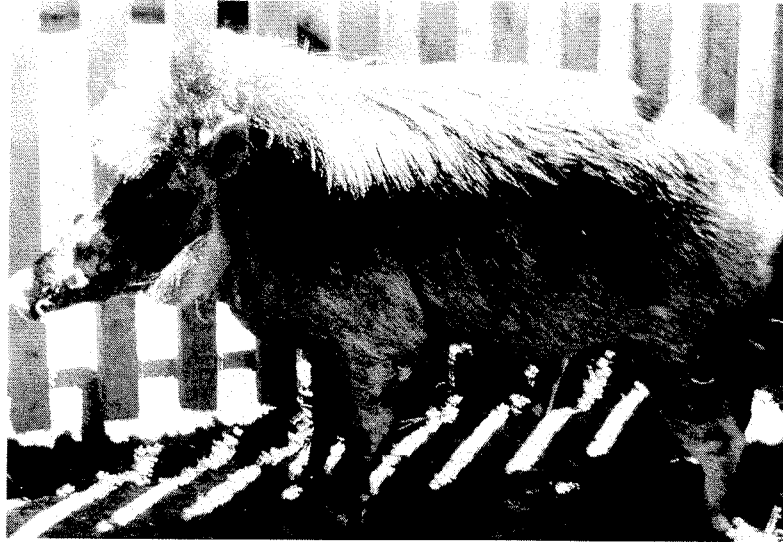


Figure 2. *Sus philippensis philippensis*, 10-year-old male, from Batangas Province, Luzon. Manila Zoo (photo W. Oliver).

Batangas Prov., S. Luzon (Fig. 2), is grey-black with hair longish on the back but sparse, abraded on the lower flanks (captive environment?), but a noticeable greyish crown tuft, which is mainly upright but leans forward toward the front, and grades into a full nuchal mane ending on the withers; long, thin creamy-white gonial tufts; a large preocular wart pair; traces of a white face band. In the living animal the face is gently concave and the snout has a very elongated appearance, contrasting with the short high facial and braincase region, and the snout disk is slightly downpointing.

A young male in captivity at Subic Bay is in process of changing from the striped juvenile to the black adult pelage. It has black and brown-ochery hairs mixed on the flanks; the crown tuft is essentially undeveloped, with just a few erect black hairs, but there is a somewhat elongated black mane from nape to loins; preocular warts are already noticeable, sparsely white-haired, with a vague whitish band between them; the white gonial tufts are very long.

BM 54.3.11.7, labelled just 'Philippines', is an infant. The body has creamy and blackish hairs mixed; on the upper half of the body, they form alternating longitudinal stripes. Underparts are whitish. Head is fawn-yellow, with darker hairs on crown.

Mindanao

FMNH 56468 and 56474, adult females: each has black bristly hair, but the hairs are very sparse, the grey skin showing through (especially markedly in 56474); a backwardly directed crown tuft is black mixed with red-brown, continuing as a short black mane which fades towards loins; long yellow gonial tufts; whitish hairs in front of eyes, but no snout band. A female in Malabon Zoo has the anterior part of the crown tuft white; its snout is convex and the disk points slightly down.

FMNH 56469, an adult male, has very sparse black bristly hair, nearly all abraded

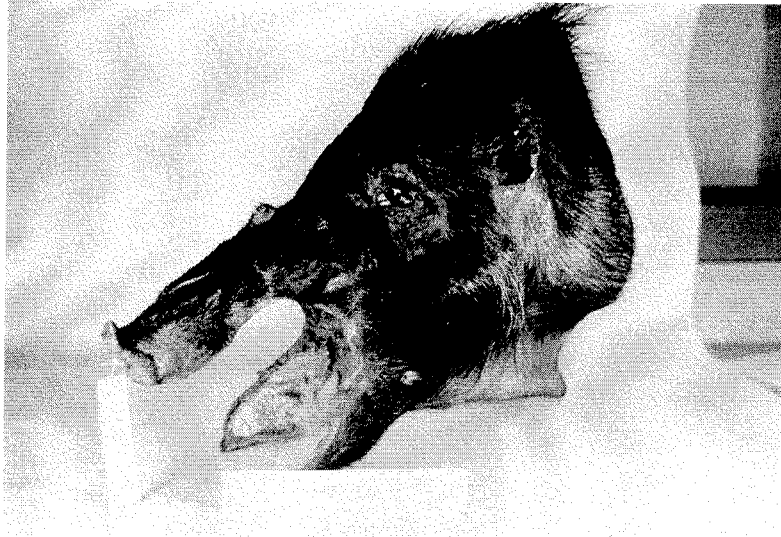


Figure 3. *Sus philippensis oliveri*, type, head-skin, FMNH 148194 from Mayapang, Rizal, Mindoro Occidental (photo L.R. Heaney).

on the back; remains of a long backwardly directed crown tuft, black mixed with dark red; very long thin gonial tufts, black mixed with deep red-brown and straw colour, overlying small warts; a preocular pair of warts; no face band. BM 91.11.28.3 (the type of *mindanensis*) and an old captive male in Dumaguete differ in having a wholly black tuft and nuchal mane; a yellow band over the snout, extending vaguely under the jaw; a slight yellow intermixture on the forehead; gonial tufts yellow. In the living male the snout is slightly convex and the disk points slightly down.

FMNH 56467, 61018, 61019, 61020, 62065 and 62066, juveniles and subadults, have a weak snout band; crown crest is entirely black; yellow gonial hairs, but no tufts. FMNH 92231 has some red hairs in the crest.

FMNH 61021, a younger juvenile, has the flank hair deep blackish red.

Mindoro

FMNH 148194, head-skin only (Fig. 3), is black; the crown tuft is elongated, the hairs straw-coloured except for their black bases; long straw-coloured hairs on incipient gonial warts; the same colour hairs are growing just behind the well-developed preocular warts. The crown-tuft continues back, but more black, as a mane at least to the nape.

Negros

FMNH 68001, 68002, 65455, 65456, 66322 and 66325, and three photos (one reproduced here as Fig. 4) of living specimens at Silliman University, adult and subadult females, have sparse bristly black hair (especially sparse in FMNH 66322 and 66325); there is little crown tuft or mane; a weak snout band in most, but strong in one of the living specimens; a white gonial spot, but no real tuft. In 68002



Figure 4. *Sus cebifrons*, pure-bred male (rear) and female (front). WUSU/CAF (photo W. Oliver).

the crown tuft has some straw-coloured hairs in it, and in 65455 and 65456 it is mixed with black and red.

FMNH 65454, adult male, has the flank hair mainly fawn-toned, straw-coloured with a few black hairs mixed in; on the underside, the black predominates; crown tuft is mainly deep red-fawn; mane is very sparse, but black, and extends to loins; white face-band is well-marked, broad; whitish gonial tufts, with no trace of gonial warts; very small preocular warts. FMNH 66325, the type of *negrinus*, differs somewhat: the body hairs are very sparse, black mixed with white-tipped hairs; on underside, the black hairs are fewer than above; there are long whitish-yellow bristles above eyes and on cheeks, and the snout band is whitish-yellow; there is a slight gonial verrucose thickening. An adult male living in a private collection in Iloilo, Panay but originating from Negros, and another at Silliman University (Fig. 4), are very like the type, but the light tips on the flanks are sparser; the crown tuft is black; they have large preocular as well as gonial warts. A living subadult male in the Silliman University collection (photo W. Oliver) has much more buffy sprinkling on the flanks, and is sharply orange-buffy on the underside; it retains a bushy tail tuft, and this is white in colour; in other specimens the tuft is largely abraded, but what remains can be seen to be white or whitish. A young male (photo W. Oliver) has medium-length black hair; crown tuft and mane are reddish; a broad white snout band; white gonial hairs; the face and snout are slightly, smoothly concave; warts are in process of development in this individual as the later photos show.

FMNH 66323, a juvenile, has less bristly hairs, with a reddish tinge; there is no white except for a line from cheek to base of forelegs, and a poorly marked snout band.

Panay

An adult female (with only three legs) living in a private collection in Iloilo City, Panay is grey-black, with buffy-white and black hairs mixed on the flanks; the crown

tuft is thick and broad, the hairs black with long white tips, upright anteriorly but leaning backward on the occiput; there are a narrow white snout-band, and short white hairs on the jaw angles. Another female, living in the collection of the Rescue and Breeding Centre at the West Visayas State University's College of Agriculture and Forestry, Lambunao, Panay has black and brown hairs intermixed on flanks; abraded remnants of a short black crown tuft, continuous with an equally abraded black mane extending to croup; indistinct short white gonial tufts; a narrow white snout band. The snout is straight and the disk points down; the crown is noticeably high.

An adult male in the same collection has dense grey-brown hair on the flanks; longer brown hair (forming a broad, short tuft in summer, which grows longer in winter) on crown, continuous with nuchal mane, which extends, shorter and blacker, along back to croup; legs are blacker than flanks; face has a narrow white transverse band; short, indistinct buffy-white tufts in gonial area; preocular warts. As in the female, the crown is high, and the disk points down, but the snout is more convex.

The piglet of these two has two pairs of thick, black stripes (one along the back, lateral to the thin median dorsal stripe, one along the flanks and haunches) on an ochery-brown ground.

Masbale. A young adult female is black, with a trace of a pale face-band, and a simple backwardly-directed toupée.

Skulls, visual comparisons

There are characteristic differences in the skulls between island samples, as follows:

Palawan, Balabac and Culion (Fig. 5A)

Skulls from these three regions may be taken together. All resemble very closely skulls of Bornean *Sus barbatus*, as described by Groves (1981): facial skeleton points forward, is extremely elongated and very slightly, if at all, concave. The male's canine apophysis is hardly developed, merely a low ridge. The malar tuberosity is nearly flat, not swollen out. Face, zygomata, braincase and occiput are all narrowed. The naso-frontal suture is saw-edged. The occiput, seen from behind, tends to be rounded above (but there is variability in this); the foramen magnum is deeply and rectangularly emarginate behind. Palate is very narrow, elongated, so that the mesopterygoid fossa is short, and ends well behind M^3 level (about two M^3 -lengths behind); the premolar rows diverge only very slightly anteriorly. M_3 and M^3 have long talons. The lateral margins of the mandibular corpora are not convex.

The positions of key landmarks (Table 1) are as in Bornean *S. barbatus*, whose facial elongation these skulls share.

Luzon, Mindanao, Catanduanes, Leyte, Samar (Fig. 5B)

These five samples may also be taken together, though only in the case of Luzon and Mindanao are sample sizes satisfactory. The facial skeleton is forward-pointing and elongated, but by no means to the same extent as in the Palawan sample,

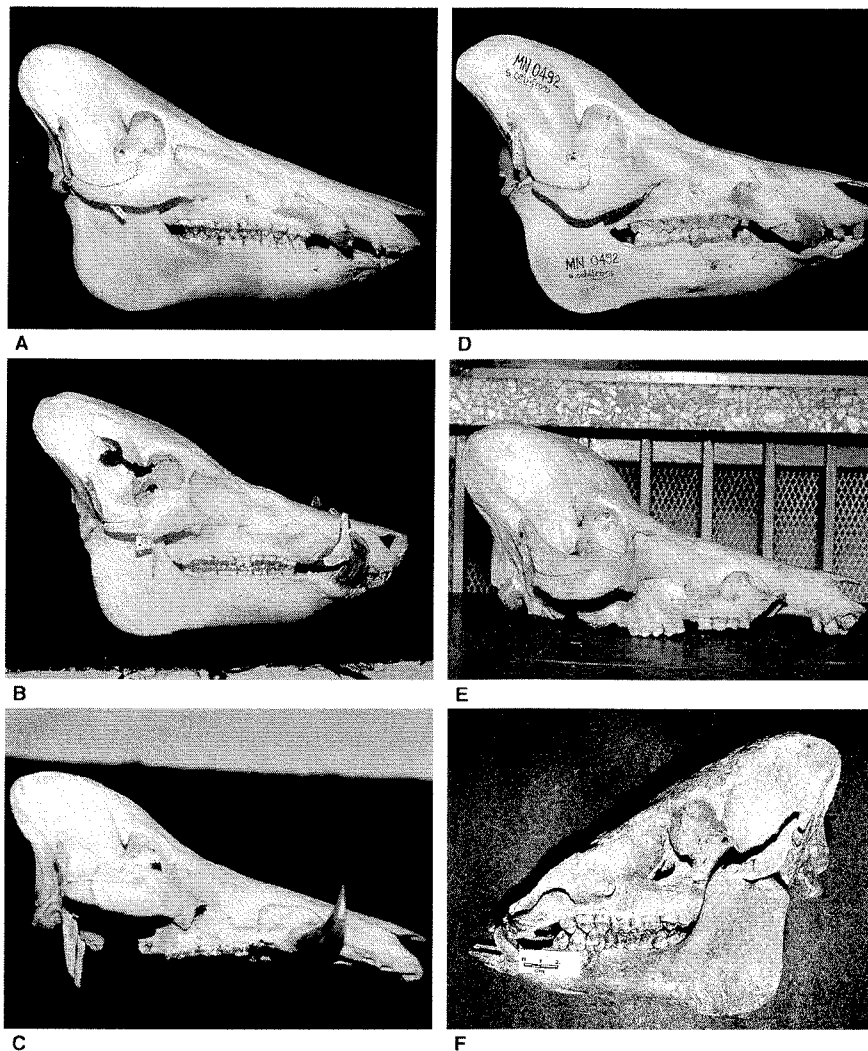


Figure 5. Skulls of Philippine wild pigs (all adult males). A, *Sus barbatus ahoenobarbus*, FMNH 62830: Iwahig, Palawan. B, *Sus philippensis mindanensis*, FMNH 56475: Cotabato, Mindanao. C, *Sus philippensis oliveri*, USNM 113247: Mindoro. D, *Sus cebifrons negrinus* FMNH 148196: Tayasan, Negros Oriental. E, *Sus cebifrons cebifrons*, BIZ. 4A: Cebu. (Photos C.P. Groves.) F, Tame pig, reputedly sired by a wild pig: Negros. (Photo P. Coumts.)

except anterior to the cheekteeth (Table 1), but there is less diastema between incisor row and canine. The whole skull is shorter, broader and higher, though not nearly as high-crowned as in *Sus celebensis*, the species to which these populations have often been referred, and more concave at the nasal root. The male's canine apophysis is prominent; in lateral view, its upper margin is rounded (in *Sus celebensis* it is rectangular). The malar tuberosity is rounded (not to the extent of *Sus celebensis*). Braincase is noticeably short. In rear view, the dorsal margin of the occipital crest is straight; the foramen magnum is posteriorly emarginate, as in Palawan, but

TABLE 1. Position of cranial landmarks perpendicular to tooththrow in Philippine pigs

	Hind edge canine apophysis	Infraorb. foramen	Anterior orbital margin	Posterior margin palate	Anterior temporal fossa margin
MALE					
Palawan	$\frac{1}{2}P^3$	$\frac{1}{4}-\frac{1}{2}M^1$	behind M^3	far beh. M^3	far beh. M^3
Luzon etc.	P^{2-3}	ant. $\frac{1}{2}M^1$	$\frac{1}{2}$ end M^3	back M^3	at M^3
Mindoro	$\frac{1}{4}P^3$	$\frac{1}{2}M^1$	$\frac{1}{2}M^3$	far beh. M^3	at M^3
Negros	$\frac{1}{4}-\frac{1}{2}P^2$	$\frac{1}{4}M^1$	$\frac{1}{2}-\frac{3}{4}M^3$	behind M^3	just beh. M^3
FEMALE AND YG. AD. MALE					
Palawan	$\frac{3}{4}P^3$	$\frac{1}{2}M^1$	behind M^3	far beh. M^3	far beh. M^3
Luzon etc.	P^{3-4}	P^1-M^1	$\frac{3}{4}M^3$	at M^3	at M^3
Leyte	$\frac{1}{4}-\frac{1}{2}P^3$	$\frac{1}{4}M^1$	$\frac{3}{4}M^3$	at M^3	at M^3
Negros	$\frac{1}{2}P^2-P^2-3$	P^1/M^1	$\frac{1}{3}-\frac{3}{4}M^3$	behind M^3	just beh. M^3

smoothly rather than abruptly, so the entire foramen is tear-shaped. The anterior part of the premolar rows are strongly concave outward. The palate ends at or only just behind M^3 level. The lateral margin of the mandibular corpus in both sexes has a convexity below the posterior premolar-anterior molar region. Skulls from Luzon and Leyte tend to have more flat-topped crowns than those from Mindanao, and those from Leyte are less concave at the nasal root. Mandibles from Samar resemble those of this group; mandibles from Leyte (young adult males only available) have the canines standing rather further in front of the premolar row.

Mindoro (Fig. 5C)

Compared to the Luzon (etc.) sample, the facial skeleton is very elongated, especially anterior to the canines, and points more downward; the concavity is exaggerated by an inflated frontal sinus, rendering the top of the crown more nearly horizontal. The canine apophyses, seen from the side, are more rectangular (but not as much so, or as large, as in *Sus celebensis*), and are more flared laterally. The malar tuberosity is more swollen. The braincase is more elongated behind the zygomatic roots. The palate is more elongated (one M^3 -length behind the back of M^3), but not to the extent of the Palawan sample.

Negros (Fig. 5D)

Compared to Luzon (etc.), all skulls from Negros have remarkable frontal inflation, continuing up to the crown (which is often—although not invariably—very high), so top of crown is horizontal (not sloping up and back as in Luzon; note that Mindoro skulls are intermediate in this respect). Canine apophyses of males are large, like Mindoro, and greatly flared laterally; malar tuberosities are swollen, even in females; the rostrum points forward, but less so than in Luzon/Mindanao. The snout is more elongated anterior to the premolars. The nasals are straight, not tending to be convex as in Luzon. Braincase is more elongated than in Luzon; whole skull is broader, especially braincase, and the occiput tends to be laterally flared. Malars are flared laterally, and angled to rostrum, not sloping evenly. The premolar rows have hardly any lateral curvature anteriorly. The palate ends about half a M^3 -length behind the back of M^3 . Foramen magnum is triangular; from

TABLE 2. Canine index (male mandibular canine, inferior surface as percent of posterior surface) in the genus *Sus*

	Range	<i>n</i>
<i>Sus scrofa</i> , <i>Sus sabbianus</i>	62-109	57
<i>Sus verrucosus</i> , <i>S. celebensis</i>	113-162	33
<i>S. barbatus</i> (Indonesia/Malaysia)	105-144	21
Palawan	111-118	2
Mindoro	145-162	2
Luzon	146-178	4
Catanduanes	162	1
Samar	160-170	2
Mindanao	139-171	7
Negros	118-146	7
Masbate	127-129	2

behind, the occipital crest is more flared than other samples, and more constricted below this. The lateral margins of the mandibular corpora often have a marked convexity below M_2 in the male, but not in the female, and the canine alveolar region is flared outward; occasional approaches to this may be seen in Luzon and, especially, Mindoro.

The skull of a Cebu pig figured by Heude (1888) and recently photographed in the Beijing Institute of Zoology (Fig. 5E) agrees with the Negros skulls in every important respect, but has a grotesquely swollen interorbital frontal region, and the muzzle is more elongated.

Dr Peter Coult's (formerly of the Victorian Archaeological Survey, Melbourne) has shown me the skull of a tame pig (male) which was killed for a feast in his honour at the end of archaeological work on Negros. He was told that the father of this animal had been a wild pig, and the skull retains the high crown and deep preorbital fossa of *Sus cebifrons* (Fig. 5F).

Metrical characters

Table 2 gives the ranges for the canine index, as defined by Groves (1981:11). The evidence for a difference between pigs from most of the Philippine islands (Mindoro, Luzon, Catanduanes, Samar, Mindanao) and *Sus barbatus*, tentatively indicated by Groves (1981), is corroborated; unexpectedly, however, those from Negros and Masbate have an index that is within the *S. barbatus* range.

The mandibular cheekteeth of the Palawan/Balabac sample (Table 3) are larger than those of other samples (in the case of P_2 , P_3 and M_1 lengths in males, the one-standard-deviation limits do not overlap those of the next largest sample), except that P_1 and (to a lesser degree) P_2 are reduced, and all teeth are relatively narrow. In Mindoro, compared with Luzon and Mindanao (males only are available), the second and especially third molars are relatively enlarged (although no measurement by itself is significantly different from any in the Mindanao sample, and only widths from Luzon). Negros specimens have small cheekteeth in general, but third molars are comparatively large: in males P_4 and M_2 are absolutely shorter than Mindanao (standard deviation limits do not overlap), and M_1 and M_2 are absolutely narrower, but in females all length measurements except M_2 and M_3 length are different, as are all molar widths—differences from Luzon are less. Mindanao and Luzon do

TABLE 3. Mandibular dental metrics of Philippine *Sus*

MALES									
Tooth	Palawan	Mindoro	Luzon	Catanduanes	Leyte	Mindanao	Negros	Masbate	Jolo
<i>n</i>	4	3	9 10	1	1	9	4	2	3
Lengths									
P ₁	7.60	8.53	5.20	8.3	9.9	8.38	6.63	6.20	8.33
SD	0.53	0.81	1.27			0.82	1.90		0.58
P ₂	12.37	10.97	11.10	11.0	12.1	10.60	9.68	10.40	11.67
SD	1.18	0.29	1.05			0.63	0.40		0.58
P ₃	14.03	11.93	11.76	13.0	13.3	11.86	10.90	11.70	12.00
SD	0.25	0.31	0.69			0.78	0.47		0.00
P ₄	13.83	13.13	12.56	13.6	13.3	12.44	10.88	12.50	13.50
SD	0.74	0.40	1.03			0.71	0.21		0.50
M ₁	16.73	13.60	13.51	15.2	14.6	13.81	13.08	13.45	14.33
SD	0.64	1.90	0.95			0.81	0.51		1.15
M ₂	20.30	18.23	16.58	18.5	18.6	17.73	15.98	16.85	17.67
SD	1.13	1.16	0.78			0.59	0.42		1.53
M ₃	31.53	29.47	25.92	26.0	26.1	26.80	25.05	24.55	32.33
SD	2.72	2.41	2.23			1.45	1.82		0.58
Widths									
P ₁	8.83	10.27	9.19	10.1	10.5	8.71	8.75	9.60	9.00
SD	0.91	1.45	0.42			0.98	0.45		0.00
M ₁	11.13	10.93	9.84	10.3	11.1	10.25	9.13	9.40	10.17
SD	1.00	0.32	0.67			0.54	0.42		0.29
M ₂	14.40	13.57	12.10	13.3	13.0	13.09	12.30	12.40	12.67
SD	1.25	0.46	0.22			0.39	0.20		0.58
M ₃	15.13	15.53	13.67	14.8	14.4	14.45	14.08	14.20	14.33
SD	1.21	0.70	0.49			1.05	0.39		0.58
Females									
Tooth	Palawan	Luzon	Catanduanes	Leyte	Mindanao	Negros			
<i>n</i>	1	6	1	4	3	6			
Lengths									
P ₁	7.0	7.65		8.65	7.38	5.63			
SD		0.80		0.77	0.82	0.41			
P ₂	9.5	10.53	11.6	11.03	10.65	8.80			
SD		0.63		0.67	0.52	0.73			
P ₃	13.0	11.33	13.0	11.78	11.23	10.23			
SD		0.64		0.65	0.28	0.80			
P ₄	13.0	11.85	13.7	12.13	12.10	10.55			
SD		0.94		0.67	0.29	0.85			
M ₁	15.0	13.23	14.9	13.93	14.00	11.47			
SD		0.87		0.85	0.62	0.87			
M ₂	18.0	16.80	17.2	17.70	17.20	15.23			
SD		0.75		0.87	0.61	1.66			
M ₃	32.0	23.63	24.4	25.05	23.80	21.27			
SD		1.04		1.77	1.33	1.62			
Widths									
P ₁	15.0	8.83	10.60	9.70	8.13	7.77			
SD		0.63		0.26	0.88	0.21			
M ₁	12.0	9.62	9.60	10.50	10.13	8.87			
SD		0.50		0.50	0.56	0.21			
M ₂	14.0	11.93	12.30	13.10	12.58	11.33			
SD		0.51		0.71	0.50	0.34			
M ₃	14.0	12.97	14.70	14.20	13.40	11.85			
SD		0.59		0.92	0.64	0.59			

not differ in proportion from each other, except that the standard deviations of M_2 width do not overlap; and Jolo is not very different from Mindanao.

Of the smaller samples, Leyte is very close to Mindanao and Luzon, but rather large (especially those of the female). The teeth of the available specimens (one male, one female) from Catanduanes are considerably larger than those from nearby Luzon, more like Mindanao, but the two posterior premolars and the two anterior molars are longer (not broader) than either. Two male specimens from Masbate are metrically close to Luzon, but with smaller anterior premolars (P_2 is as small as in Negros), and have the narrow premolars of Negros. Finally three male specimens from Jolo, in the Sulu Archipelago, are very large, with especially elongated third molars: in proportions they resemble no other sample very closely. The Jolo measurements were kindly supplied by Dr Peter Grubb; I have not been able to study any material personally.

Maxillary cheekteeth add no information to that given by mandibular teeth.

Skull measurements (Table 4) reveal distinct differences. Palawan skulls are very large (but not as large as Bornean *S. barbatus*), but Greatest Skull Length exceeds other samples to a lesser degree than Condylbasal Length, indicating a less backwardly extended occipital crest (a difference from Bornean *barbatus*); but they are narrower, both zygomatic arches and, more especially, Occipital (crest) Breadth. Mindoro skulls, compared to those of Luzon and Mindanao, are broader and have very deep malars, and skull height is greater: no measurement, by itself, absolutely distinguishes Mindoro from Mindanao, but proportionally (see below) they can be differentiated. Mindanao males, but not females, are significantly bigger than Luzon, and somewhat higher. The single (male) skull from Catanduanes is noticeably larger than those from Luzon; it would probably be lost in the sample from Mindanao, except perhaps for its relatively greater breadth. Wild Negros skulls are smaller than any other in both sexes; they have relatively broader zygomata, but not occipital crests; they are (relatively) much higher; the upper toothrow is significantly shorter. It must be noted that the skull of a Negros male from captivity is much larger than any other (Greatest Length 356 mm) though in proportion; great phenotypic plasticity in size in pigs has been previously noticed (Groves, 1981).

As measured by Greatest Skull Length, different populations show different degrees of sexual dimorphism. Males average 109.6% of females in Palawan, 118.4% in Luzon, 128.0 in Mindanao, 126.5 in Negros. In condylbasal length these figures are, respectively, 109.6, 114.8, 122.1, 118.6.

The two mandibular diastemata differ in their relative size in different samples in males. In Palawan, Mindoro, Negros and, unexpectedly, the single specimen from Catanduanes, the P_{1-2} diastema is larger than the C_1-P_1 diastema; in Luzon and Mindanao, the C_1-P_1 diastema is almost always larger (3 exceptions in 9 specimens). In females, the two diastemata are about equally long.

Discriminant analysis

The plots of first and second Discriminant Functions are shown in Figure 6. Crania of *Sus celebensis* are well separated from those from the Philippines; within the Philippines group, the clusters from Palawan, Negros and Luzon/Mindanao/Mindoro are somewhat separate (Fig. 6A). A skull from Leyte, entered as an unknown, falls close to Luzon; one from Jolo is, interestingly, between Mindanao

TABLE 4. Craniometrics of Philippine *Sus*

MALES									
Measurements	Palawan	Mindoro	Luzon	Catanduanes	Mindanao	Tawitawi	Jolo	Negros	Cebu
Skull length	367.0	340.0	325.2	338.0	347.3	343.0	332	306.8	309
SD	9.82	9.54	18.34		20.07		8.02		
<i>n</i>	5	3	15	1	12	1	1	5	1
Condylbasal I.	323.4	292.3	277.8	284.0	291.5	301.0	292.7	259.5	264
SD	8.35	12.06	9.19		11.37				
<i>n</i>	5	3	13	1	11	1	3	2	1
Bizygomatic br.	147.0	151.0	139.0	150.0	146.0	139.0	142.7	138.3	146
SD	7.96	2.65	6.99		11.37		4.92		
<i>n</i>	4	3	15	1	11	1	3	4	1
Occipital br.	68.0	82.0	81.1	91.0	81.5	77.0	75.0	77.5	90
SD	5.48	5.66	6.92		6.06				
<i>n</i>	4	3	15	1	11	1	1	2	
Zygomatic depth	35.5	38.6	32.0	29.5	33.0	34.8		26.0	25.7
SD	5.59	7.64	2.91		3.61		0.92		
<i>n</i>	2	2	10	1	11	1		4	1
Skull height (+jaw)	206.5	209.5	185.6		200.5		169.0	188.2	
SD	20.31	14.85	16.19		17.31		4.32		
<i>n</i>	4	2	7		6		1	5	
P ² -M ³	105.7	98.0	89.2	99.0	91.8	87.0	91.0	82.7	79
SD	8.71	4.36	4.30		6.59		4.61		
<i>n</i>	6	2	19	1	13	1	2	7	1
C ₁ -M ₃	157.2	149.5	130.9	135.0	141.3		148.0	119.7	
SD	4.49	14.85	6.08		4.30		3.00	4.97	
<i>n</i>	5	2	8	1	9		3	6	
FEMALES									
Measurements	Balabac	Palawan	Luzon	Mindanao	Negros				
Skull length	348.5	335	274.7	271.3	242.6				
SD			6.47	5.38	11.10				
<i>n</i>	2	1	6	4	7				
Condylbasal I.	310.5	295	242.0	238.8	218.8				
SD			6.52	3.59	6.01				
<i>n</i>	2	1	5	4	6				
Bizygomatic br.	128.0	122	115.5	117.0	111.0				
SD			3.94	2.16	5.86				
<i>n</i>	2	1	6	4	8				
Occipital breadth	63.5	62	59.7	59.5	52.8				
SD			5.20	8.79	4.22				
<i>n</i>	2	1	6	4	6				
Zygomatic depth			25.3	25.3	21.4				
SD			2.41	0.85	3.34				
<i>n</i>		6	4	8					
Skull height (+jaw)	176.0	177	154.4	150.8	145.8				
SD			8.32	3.50	9.89				
<i>n</i>	2	1	5	4	6				
P ² -M ³	101.0	100	89.7	90.0	78.0				
SD			2.34	2.00	3.00				
<i>n</i>	2	1	6	4	9				
C ₁ -M ₃	149.5	142	111.4	116.3	98.0				
SD			4.27	1.53	2.19				
<i>n</i>	2	1	5	4	8				

and *Sus celebensis*, though closer to the former. A contrast between palate length and skull height accounts for much of the discrimination along the first axis; skull size and postorbital constriction along the second.

TABLE 5. Comparative nomenclature of Philippine pigs

Island	Sanborn, 1952	Groves, 1981	This paper
Palawan, Calamianes	<i>S. barbatus ahoenobarbus</i>	<i>S. barbatus ahoenobarbus</i>	<i>S. barbatus ahoenobarbus</i>
Luzon	<i>S. celebensis philippensis</i>	<i>S. barbatus philippensis</i>	<i>S. philippensis philippensis</i>
Mindanao	<i>S. celebensis philippensis</i>	<i>S. barbatus philippensis</i>	<i>S. philippensis mindanensis</i>
Mindoro	(not considered)	(not considered)	<i>S. philippensis oliveri</i>
Negros group	<i>S. celebensis negrinus</i>	<i>S. barbatus cebifrons</i>	<i>S. cebifrons subsp.</i>

For maxillary teeth (Fig. 6B), the small samples of *S. celebensis*, from Palawan, and from Negros surround a central cluster, within which the Mindoro sample is better separated than are the Luzon and Mindanao samples. A skull from Leyte is closest to Luzon; one from Basilan is closest to Mindanao. No particular arrangement of measurements is obviously responsible for the discrimination.

For mandibular teeth (Fig. 6C), the same three samples are again peripheral, but this time separate Luzon, Mindanao and Mindoro clusters also appear – the Mindoro sample in fact is better separated than the Palawan sample. Two Jolo specimens are curiously closer to Palawan; one Masbate specimen is close to Mindanao, the other falls between it and Negros. Again, no obvious arrangement of the raw metrics stands out as responsible.

Cladistic analysis

The characters used, and their apparent polarity (except for canine shape, as noted above under Methods), using *Potamochoerus* as outgroup, are listed in Tables 6 and 7. The PAUP Heuristic Search produced a single shortest tree (length 104, C.I. 0.49). This was bootstrapped, and the result is shown in Figure 7. *Sus barbatus* and *S. verrucosus* form the sister clade to all others. The next most distinct species is *Sus celebensis*; followed by *S. cebifrons* (the Heude skull from Cebu and the Negros specimens were coded separately, as an experiment), while *S. scrofa* and the remaining Philippines taxa formed the terminal clade. It should be noted, however, that bootstrap values are not high; the highest being the *S. barbatus* and *S. verrucosus* clade (83%), followed by association of the Luzon, Mindanao and Mindoro samples (69%), and, within that grouping, of Luzon with Mindanao (again 69%). Associating the Cebu and Negros components of *S. cebifrons* in the same clade adds one step to the tree length and reduces the consistency index to 0.480.

It should be noted that *Sus scrofa villatus* was the form of *S. scrofa* initially used to code characters in the analysis, but skulls of other subspecies (*S.s. scrofa*, *S.s. cristatus*) were subsequently coded, using photographs, and in all cases were similar to *S.s. villatus*.

The *Sus barbatus/verrucosus* clade is characterised by the very narrow skull (char. 13). The *S. scrofa/celebensis/Philippines* clade is characterised by derived states of char. 14 (shortened palate), 23 (smaller size), 28 (more anterior placement of orbital margin) and 29 (more anterior placement of temporal fossa). The *Sus philippensis* clade has derived conditions of characters 8 (gonial whorls) and 19 (convex nasals, parallel to *S. barbatus*), a more highly derived condition of character 29 (temporal fossa still more anteriorly placed), and reversals of characters 3 (crown tuft developed)

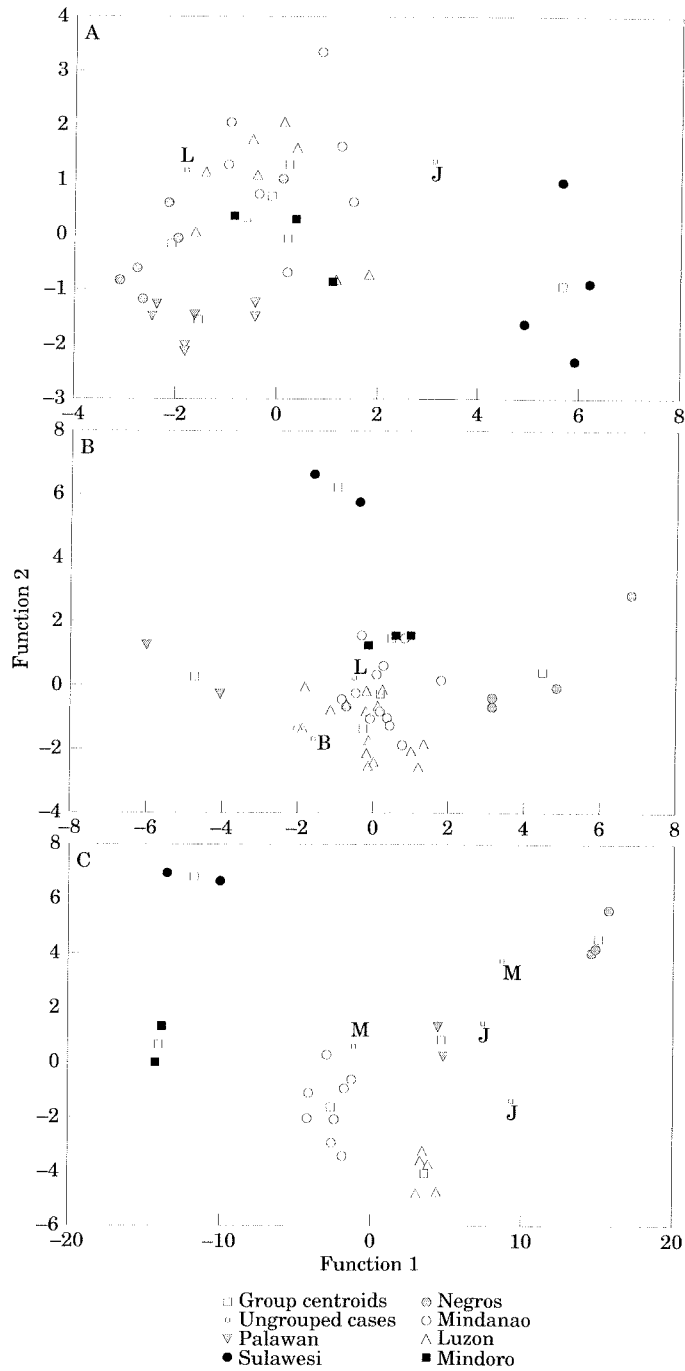


Figure 6. Plots of first and second Discriminant Functions for craniodental variables of Philippine pigs and *Sus celebensis*. A, Six cranial variables. DF1 = 77.39% of variance, DF 2 = 16.71%. B, 14 variables of maxillary dentition. DF1 = 41.64% of variance, DF2 = 31.70%. C, 14 variables of mandibular dentition. DF1 = 77.34% of variance, DF2 = 13.53%.

TABLE 6. Characters used in cladistic analysis

1.	Number of hair types on body (1; 2)
2.	Mane extension (to rump; not to rump)
3.	Crown tuft (elaborate; small; absent)
4.	Snout band (absent; weak or variable; bold)
5.	Snout disk direction (points more downward; less downward)
6.	Preocular warts (absent or rudimentary; small; large)
7.	Gonial warts (absent or rudimentary; present)
8.	Gonial hair whorls (absent or rudimentary; large; long thin). UNORDERED
9.	Facial skeleton direction (faces forward; slightly downward; more downward)
10.	Facial skeleton length (elongated; less long; short)
11.	Male canine apophysis (huge, rectangular; large, rectangular; moderate, rounded; very reduced)
12.	Malar tuberosity (inflated; rounded; flat)
13.	Zygomata (flared; less flared; narrow)
14.	Palate (elongated; fairly long; fairly short; short)
15.	Anterior premolar divergence (yes; slight; no)
16.	Mandibular lateral swellings (large; slight; absent)
17.	Crown height (low; fairly high; very high)
18.	Crown shape (rounded; flat)
19.	Nasals (straight; fairly convex)
20.	Premolars (large; relatively small; small)
21.	Posterior molars (elongate; not elongate)
22.	Dental size (large; smaller)
23.	Overall size (large; medium; small)
24.	Sexual size dimorphism (none; moderate; great)
25.	P_{1-2} diastema cf. C_1-P_1 (>; <)
26.	Posterior rim of male C_1 apophysis (posterior; medium; anterior)
27.	Position of infraorbital foramen (anterior; moderate; posterior)
28.	Position of anterior orbital margin (posterior; moderate; anterior)
29.	Position of anterior end temporal fossa (posterior; moderate; anterior)
30.	Male C_1 index (moderate or low; high)

Character states are listed from primitive to most derived. Except for no. 8, all characters are ORDERED

TABLE 7. Data set for cladistic analysis

outgroup	0000000000	0000000000	0000000001
<i>scrofa</i>	0021100003	3223220000	1021020210
<i>celebensis</i>	0022010000	0002102002	0021000212
<i>barbatus</i>	0022010000	3220220112	0000002002
<i>oliveri</i>	??00121221	1011002111	001?012123
<i>philippensis</i>	1100121202	2113001110	1121121223
<i>mindanensis</i>	1101110202	2113001010	1112121223
<i>negrinus</i>	0012100012	1002212000	0122021212
<i>cebyronus</i>	??????01	10022?2000	012??1001?
<i>verrucosus</i>	0022021100	2010200102	0002022002
@			
*	0000000000	0000000000	0000000000

and 15 (premolar rows diverge anteriorly); within this clade the Luzon and Mindanao taxa share derived states of characters 12 (rounded malar tuberosity) and 25 (lower canine- P_1 diastema longer than P_{1-2} diastema), and reversals of no 17 (high crown), by contrast to the Mindoro form; the condition of characters 1 (hair types) and 2 (mane) in Mindoro is unknown. *S. philippensis* shares with *S. scrofa* the derived states of char. 4 (rather reduced snout band) and 13 (reduced zygomatic flare).

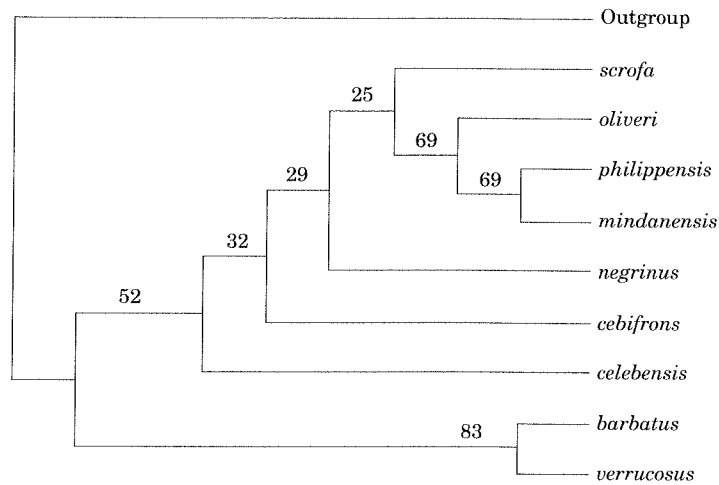


Figure 7. Cladogram of Philippine pigs and related taxa. Tree length = 104; Consistency Index = 0.49.

The only character separating the *S. scrofa/philippensis/cebifrons* clade from *S. celebensis* is no. 26 (anterior position of canine apophysis).

None of the other Philippines taxa was closely associated with the Luzon, Mindanao and Mindoro grouping. The highest bootstrap value associating *S. cebifrons* with the group is 32%. Associating Cebu and Negros in a clade with *S. scrofa* gives a tree length of 114 and a consistency index of 0.48.

Making a clade associating Negros and Cebu with *S. celebensis*, as in Sanborn (1952), adds 5 to the tree length and reduces the consistency index to 0.47.

Finally, making *S. scrofa* the sister taxon to all other *Sus* increases tree length by 6 steps and reduces the consistency index to 0.46.

DISCUSSION

The results of all these comparisons indicate that the Philippines pigs excepting those from the Palawan region (including Balabac and Calamianes) cannot be assigned to *Sus barbatus*, contra Groves (1981); the similarities reflect shared retention of primitive features. Moreover, they are not even closely related to *S. barbatus*, but instead represent one or (more probably) two ancient branches of the *S. scrofa* lineage. They divide into two highly distinct groups: one contains pigs from Negros (and probably those from Panay [on the evidence of the external appearance] and Cebu [on cranial evidence]), the other those from Mindoro, Luzon and Mindanao, to which on the limited evidence can be added Catanduanes, Leyte and Samar. There is, as yet, no evidence as to the placement of the pigs of the Sulu Archipelago.

The distinction between Negros and the rest is so clear and consistent that recognition at full species level is called for. The Cebu specimen assorts separately on the cladogram (Fig. 7) from those from Negros, and few convincingly derived conditions characterize either (whether alone or together), except perhaps for the

swollen frontals. *Sus cebifrons*, as a combined species must be called, stands as the plesiomorphic sister-group of *Sus philippensis* plus *Sus scrofa*.

The Palawan (including Balabac and Culion) pig, though referable without any doubt to *S. barbatus*, is obviously subspecifically distinct from the Indonesian/Malaysian subspecies, as previously recognized by Groves (1981).

The prior available name for the other species (the widespread Philippines species) is *Sus philippensis* Nehring, 1886, first described from Luzon. Within this species, subspecies from Mindanao and Mindoro should be recognized. For the Mindanao form the name *Sus mindanesis* Forsyth Major, 1897 is available. The Mindoro form has never been described; a new subspecies is described below.

The karyotypes, in so far as they are known, are consistent with the morphological conclusions (de Haan *et al.*, 1993). The basic karyotype of the genus *Sus* is $2n = 38$, and there are very few differences between species in chromosome morphology. Two fusions, 15/17 and 16/17, occur in different geographic samples of *S. scrofa*, reducing the number to 36. The three available pigs from Luzon and Mindanao were homozygous for a fusion previously unknown in the genus, 13/16; a specimen said to be from Mindoro did not possess this fusion, but the locality of the specimen, supplied by a hunter and physically more resembling a Palawan pig, is in question. (Attempted karyotyping of a Negros pig failed).

It is of interest that the 13/16 fusion characterises two other members of the Suidae, *Phacochoerus africanus* and *Babyrousa babyrussa*. Two alternative interpretations of the Philippine pig karyotypes are therefore possible: (1) the plesiomorphic suid karyotype is $2n = 38$, and the 13/16 fusion has occurred independently in Philippine *Sus*, in *Phacochoerus* and in *Babyrousa*; (2) the plesiomorphic suid karyotype is $2n = 36$, and this has been retained by Luzon and Mindanao pigs, fission having occurred in other *Sus* (and in *Potamochoerus* and *Hylochoerus*) independently. The first interpretation seems much the more probable.

Such a result might be expected on palaeogeographic grounds (Heaney, 1986). Negros, Cebu and Panay are separated by shallow water (<120 m deep) from each other, but by deep water from the other Philippine islands. Similarly, the Calamianes, Palawan and Busuanga are joined by shallow seas and separated from the nearest of the other Philippine islands, Mindoro, by deep water (485 m); while Mindanao, Leyte and Samar are connected by a <120 m shelf, as are Luzon and Catanduanes. Only slightly deeper water (140–145 m) separates the Palawan group from the Sunda Shelf, and the Luzon and Mindanao groups from each other. This leaves four isolated land masses at times of the lowest Pleistocene sea levels: Sundaland including Palawan; Mindoro; Luzon plus Mindanao; and the Negros group (Fig. 8) The wild pigs follow these divisions rather closely, except that the Mindoro taxon seems, on present evidence, to be less well differentiated than one might predict.

The general pattern of mammalian geography in the Philippines accords in part, but not completely, with this picture (Heaney, 1986). The Palawan group stands completely apart from the other Philippine islands, and is connected, if distantly, to Sundaland. On the other hand the Negros group is not well separated; Heaney (1986) remarks, however, that its fauna is poorly known and, on what evidence there is, depauperate. The mammal fauna of Mindoro is close to that of Luzon, with perhaps some indication of an influence from Palawan; presumably the narrowness of the intervening straits has allowed faunal exchange, overriding any effect of isolation because of their depth.

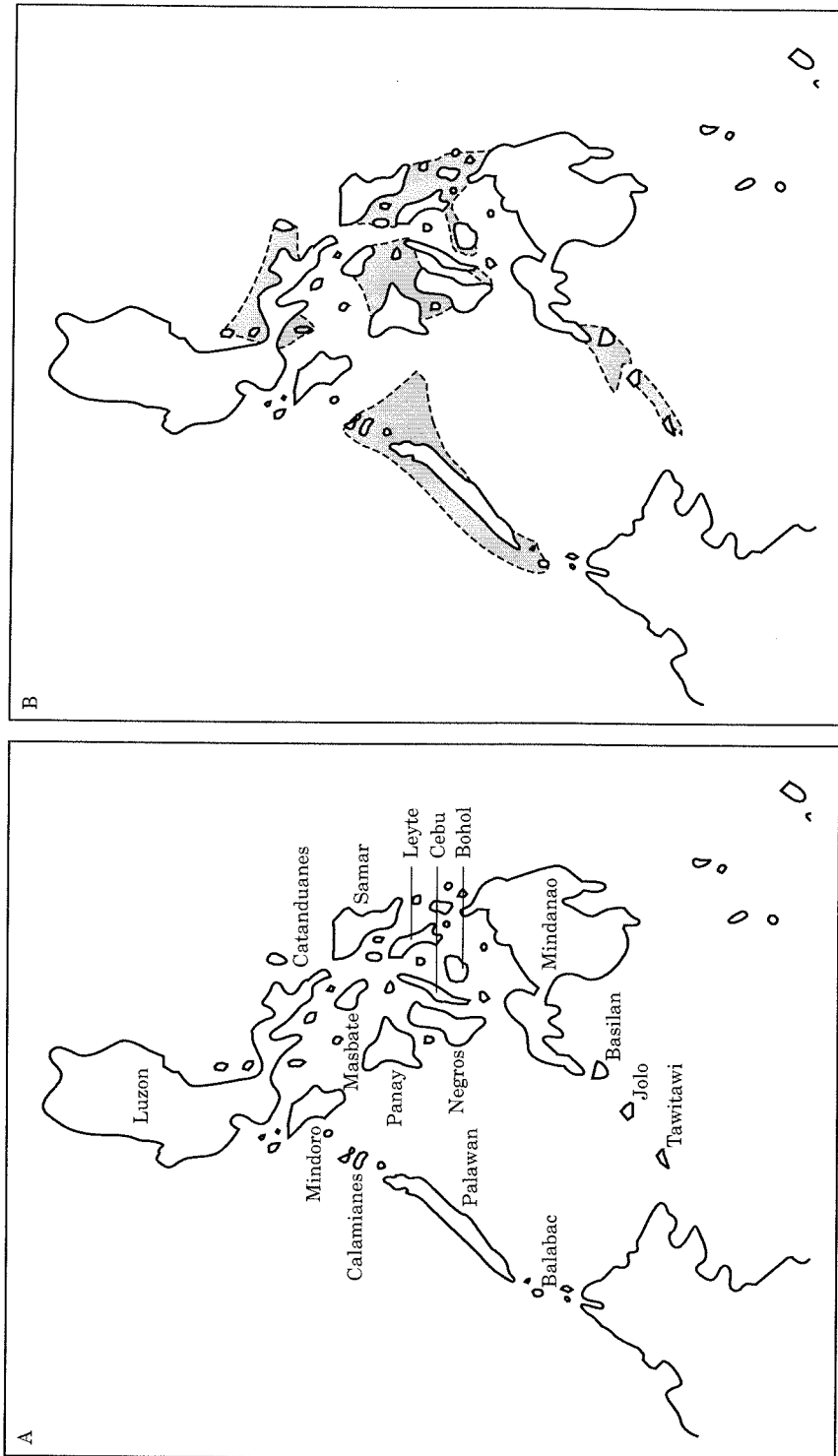


Figure 8. Map of the Philippines, to show (A) islands referred to in the text and (B) shallow-water connexions (stippled).

CONCLUSIONS

A new taxonomy of the genus *Sus* in the Philippines follows.

Sus barbatus Müller, 1838

Diagnosis. See Groves (1981:75-6).

There is a single Philippine subspecies: *Sus barbatus ahoenobarbus* Huet, 1888

Synonyms: *calamianensis* Heude, 1888; *palavensis* Nehring, 1889; *balabacensis* Forsyth Major, 1897.

Diagnosis. A subspecies of *S. barbatus* of small size, otherwise resembling Bornean *S.b. barbatus*.

Distribution. Balabac, Palawan, Calamianes group.

Notes. Heude (1888) was unaware of Huet's name given to Palawan pigs, but by 1892 had learned of its priority; nonetheless he considered it likely that his taxon, from the Calamianes, was distinct.

Sus philippensis Nehring, 1886

Diagnosis. A species of *Sus* of karyotype $2n = 36$ (as far as is known) with, in the male, an ultra-verrucose type of mandibular canine (canine index 139-178) and 2 pairs of warts; skin grey, body hair black; a long, full crown tuft and nuchal mane, but no mane along dorsum of body; snout band often absent, at most a thin yellow or white transverse band; gonial hair tuft very long and thin, largely white or yellow. Skull with deep, sharply bordered preorbital fossa. Facial skeleton somewhat elongated (more than in *S. celebensis* or *S. scrofa* but not comparable to *S. barbatus* or *S. verrucosus*), somewhat concave at nasal root; nasal slightly convex; malar tuberosity greatly swollen. Braincase high-crowned, sloping downward to facial skeleton; occipital crest extended backward; anterior margin of temporal fossa perpendicularly above M^3 or just behind it. Foramen magnum teardrop-shaped. Teeth relatively large; maxillary premolar rows curve outward anteriorly. M^3 very short, with four major cusps and a small 5th cusp; M_3 with three small lobes. Maxillary canine apophysis of male prominent, though less so than in *S. celebensis*, its posterior edge above level of P^2 - P^3 boundary or of P^3 . Lateral margin of mandibular corpus with convexity below posterior premolars.

Notes. Heude (1892, 4:117) was well aware of the canine difference between Philippine and other pigs. He divided the males' mandibular canine morphology in Asian pigs into three types, as follows:

(1) *The Internal or Superior Spiral*, directed toward the median longitudinal plane of the skull, and above the horizontal plane of the toothrow. The 'section' (meaning the angle between the posterior and inferior faces) is obtuse; the posterior face is twisted towards the postero-internal corner. This is the form seen in the *scrofa* group, and also in *Babirousa*.

(2) *The External or Inferior Spiral*, whose point is directed inferiorly and away from

the median plane. The section is a rightangle; the posterior face is twisted towards the antero-internal corner. This is the form seen in the Philippine pigs, which he referred to a special genus *Nesosus*, which he divided into numerous species, all illustrated but only a few of them actually described.

(3) *The Flat or Circular Spiral*, in which the point is directed still lower, but in the plane of its implantation. The section is acute; the posterior face is directed straight back in a circle. This is seen in the Indonesian pigs, which he divided into three genera *Verrusus* (=the modern species *Sus verrucosus*), *Microsus* (= *S. celebensis*) and *Rhinosus* (= *S. barbatus*).

His illustrations of these canines (Heude, 1892, Plate XXIX^c) are very detailed and seemingly accurate. I measured with a ruler the 'external' (=inferior) and posterior faces in his figures and calculated canine index (as in Groves, 1981) as follows: *Sus inconstans* 146, *megalodontus* 143, *effrenus* 154, *arietinus* 133, *mainitensis* 150, *crassidens* 146. Except for *arietinus*, these fall within the range for *Sus philippensis* as measured on museum specimens (see above); they contrast with the two other pigs depicted on the same plate, *S. bucculentus* of Indochina at 114, and *Sus calamianensis* (= *S. barbatus ahoenobarbus*, see above) at 120.

1. *Sus philippensis philippensis* Nehring, 1886

Synonyms: *marchei* Huct, 1888; *effrenus*, *frenatus*, *microtis*, *minutus* and *jalaensis* Heude, 1892.

Diagnosis. A subspecies of *Sus philippensis* with crown tuft greyish, with anterior fringe directed forward; facial warts relatively large; gonial whorls white; skull small in size in male; facial skeleton not downpointing; braincase shortened, relatively flat-topped; palate ends level with M³; P₁ generally closer to P₂ than to canine.

Distribution. Luzon.

Notes. Heude's species *Sus effrenus* and *Sus frenatus* were both from Jala-Jala, Laguna de Bay. They were distinguished from each other by a few skull features (described from 3 and 4 skulls respectively), but chiefly by the absence and presence, respectively, of a white facial band. *S. microtis*, from Bataan, was distinguished (on the basis of a single skull with head-skin) by its small ears, very small premolars, and a few skull details. *S. jalaensis*, by inference (but not explicitly) from Jala-Jala, was stated (1901, 5:87) to be distinguished by its very simple posterior molars.

Taylor (1934) lists the names *arietinus* (with a query) and *conchyvorus* of Heude in the synonymy of this taxon, but no locality is given by Heude for either of these putative taxa.

2. *Sus philippensis mindanensis* Forsyth Major, 1897.

Synonyms: *inconstans* Taylor, 1934 (see below, under Notes).

Diagnosis. A subspecies of *Sus philippensis* closely resembling nominotypical *S.p. philippensis*, but differing in the following features: crown tuft black mixed with red-brown, or may be white anteriorly, and apparently with no forwardly-directed component; facial warts small; gonial tuft yellow or yellow mixed with black; skull size much larger in male, but not in female (hence more sexually dimorphic); braincase more rounded.

Distribution. Mindanao; almost certainly also Balabac and Leyte.

Notes. Taylor (1934) lists the name *Sus inconstans* Heude as applying to Mindanao pigs, but I cannot find any locality for this name anywhere in Heude's works.

3. *Sus philippensis oliveri* **subsp. nov.**

Holotype. FMNH 148194, skull and head-skin, from Mayapang, Rizal, Mindoro Occidental, Philippines (Fig. 3).

Paratypes. ZMB 4886, skull only, from Calapan; USNM 113247, skull only ('Mindoro') (Fig. 5C). An immature specimen (skull length 300 mm) from Wazijan, Mindoro Oriental, is in the Philippines National Museum, Manila (A.A. Macdonald, pers. comm.).

Diagnosis. A subspecies of *S. philippensis* with (in the only known skin) crown tuft black mixed with straw-coloured hairs, and no forwardly-directed component; preocular warts well-developed; gonial tuft straw-coloured; skull in male (on the evidence of three specimens) large as in *S.p. mindanensis* (female unknown); facial skeleton more elongated and downpointing; braincase higher, more flat-topped, set off from facial slope by greater frontal inflation; malar tuberosity more inflated; canine apophysis larger, extending more posteriorly; palate ending behind M^3 ; P_1 closer to canine than to P_2 ; anterior premolars reduced, posterior molars enlarged.

Distribution. Mindoro.

Notes. Three skulls and a single head-skin do not constitute abundant evidence on which to describe a subspecies. Nonetheless the three skulls are alike, and differ consistently from all other Philippines skulls, and the head-skin likewise falls outside the range of described Philippines taxa. Given the conservation crisis in the Philippines, further material of this new subspecies is not likely to become legally available in the near future.

A fourth skull, the immature skull in the Philippines National Museum mentioned above, has the third molars in process of erupting. Measurements (kindly taken by Dr A.A. Macdonald and communicated by Ms Elenita de Vera-Alba) are: Skull length 300, Condylbasal 268, Bizygomatic breadth 135, Occipital breadth 63, C_1-M_3 130 mm.

Etymology. It is a great pleasure to name this new subspecies for Mr William Oliver, Chairman of the Pigs and Peccaries Specialist Group of the Species Survival Commission of IUCN, who has worked tirelessly for the worldwide conservation of the Suidae and other animals, in the Philippines and elsewhere, and at whose urging this study was undertaken.

4. *Other populations*

Samar. Dental samples from this island differ from that from Mindanao, to which it is closest geographically, in their longer and broader anterior premolars, and from the Luzon sample in their larger molars in addition. The canine apophysis in females does not extend as far back as in Luzon or Mindanao. Further material will clarify whether it represents a separate subspecies, or like Leyte should be placed in *mindanensis*.

Catanduanes. On the evidence of a single skull, the Catanduanes population fits more closely with *mindanensis* than with nominotypical *philippensis*, although on geographic grounds it should go with the latter; the skull is broader (especially the occiput) than Mindanao skulls. The teeth are large, rather more like *mindanensis*, or even more so the Leyte sample.

Jolo. Male dentitions from Jolo, in the Sulu archipelago, are large like Mindanao but with an exceptionally long third lower molar. The overall proportions of the toothrow are quite different from those of other taxa (Table 5), and further material is needed to confirm whether this population represents a separate subspecies, or belongs to this species at all (Fig. 6A, C).

Bohol. A skull in the Philippines National Museum (measurements taken by Dr Alastair Macdonald, communicated by Ms Elenita de Vera-Alba) from Mabin, Bohol ('male native pig') is as follows: Skull length 298, Condylbasal 281, Bizygomatic breadth 132, Occipital breadth 64, C_1-M_3 136, M_3 length 33 mm. The canine index is 80 which, coupled with the small size and (especially) the narrow occiput, indicates that this would be a domestic pig, which might in fact be the significance of 'native' in this context. Dr Macdonald's note, "deep suborbital depression of *Sus celebensis* type", suggests however that, as in Negros (see below), there could be intermittent gene-flow from the local wild population (so far unknown in this case).

Sus cebifrons Heude, 1888

Diagnosis. A species of *Sus* with, in the male, less ultra-verrucose mandibular canines than *S. philippensis* (index 118-146), and only very small facial warts. Skin grey-black; body hairs mostly black in the female and subadult male, fawn mixed with black in the adult male; usually little crown tuft, black mixed with red or straw-coloured hairs, or wholly deep red-brown; mane sparse, extending back to loins, black or red; snout-band may be weak in female, but very broad and well-marked, white or whitish-yellow, in male; gonial tuft short and wide, white, in male, but virtually absent, marked only by a white spot, in female. Skull small in both sexes; sexual size difference very marked. Facial skeleton points more or less forward; nasal root markedly concave; nasals straight, not convex. Malar tuberosity strongly swollen, even in female, so that anterior face of malar faces forward instead of sloping into maxilla; zygomatic arches flare laterally. Skull markedly high-crowned; upper surface of braincase horizontal, angled to interorbital slope; braincase long; anterior margin of temporal fossa just behind level of M^3 . Foramen magnum triangular in form. Canine apophysis large, flaring, but its posterior edge level only with P^2 ; palate ends just behind M^3 level; premolar rows diverge little if at all in front; lateral mandibular convexities marked in male, but poorly expressed in female. Teeth small; P_1 close to canine; premolars not reduced; posterior molars long and narrow.

Distribution. Known from Cebu (evidence of type skull), Negros (evidence of living specimens as well as skins and skulls), Panay (evidence of living specimens) and probably Masbate (evidence of a living specimen and of mandibles).

Notes. Judging by the labels of the Cebu skull in the BIZ, Heude (1892) evidently intended to include this species in his restricted concept of *Nesosus* ('External or Inferior Spiral' type of canine), but it does not fit the diagnosis. He distinguished it

from other Philippine species by its peculiar 'bossue' (literally hump-backed) skull: "Il a vraiment l'aspect exagéré d'un crâne d'Orang-outan". He noted its short high canine apophysis and the wide occiput that in fact characterizes many (not all) specimens from Negros as well as Cebu.

Specimens from Panay appear (on rather sparse evidence) to differ from those from Negros and Masbate externally in the greyer rather than predominantly black flank hair, the much more prominent crown tuft in the female and better developed mane in the male, and the more developed, but narrow, white snout band. Cheekteeth of Masbate specimens average very slightly larger than those from Negros, except for P_2 and M_3 , and its noteworthy that two dentitions fall away from Negros in the direction of *S. philippensis* (Fig. 6C); is it possible that Masbate pigs are mixed with *S. philippensis* or – more likely – subject to gene-flow from domestic pigs?

This species differs from *S. philippensis* mainly by primitive retentions.

1. *Sus cebifrons cebifrons* Heude, 1888

Diagnosis. The single available cranium, BIZ 4A, differs from the Negros sample in its longer diastema; anterior orbital margin placed behind the level of the toothrow and canine apophysis above P^3 ; frontals between orbits grossly swollen; skull, especially occiput, broader than Negros specimens; posterior end of preorbital fossa more square, vertical. The canine apophysis is very high and convex, and extends further back along the toothrow. Some of these features reflect the extreme old age of the specimen; older skulls from Negros, for example, have broader occipital crests than younger.

Distribution. Cebu.

2. *Sus cebifrons negrinus* Sanborn, 1952

Diagnosis. Frontal convexity less marked than in the Cebu cranium, and face less elongated, but infraorbital foramen placed further back; occiput narrower. The posterior end of the preorbital fossa is more rounded.

Distribution. Negros.

SUMMARY

Study of skins, skulls and living examples of wild pigs from the Philippines has shown that *Sus barbatus* is found only on the Palawan group; the taxa on the other islands represent two endemic species, which belong not to the *barbatus/verrucosus* species group but to the *celebensis/scrofa* group. *Sus philippensis* and *Sus cebifrons* probably do not form a monophyletic group. The former is divisible on present evidence into three subspecies, one of them here described as new; the latter may not be monotypic, but evidence is insufficient to be certain. Multivariate analyses of cranial and dental measurements, cladistic analysis of all characters studied, and published chromosomal data, all point towards these same conclusions.

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REFERENCES

- Alcasid GL. 1970.** *Checklist of Philippine Mammals*. Manila: National Museum of the Philippines.
- de Haan NA, Bosma AA, Macdonald AA, Oliver WLR. 1993.** A species of wild pig in the Philippines with a type of centric fusion translocation new to *Sus*: 13/16. In: Bosma AA, ed. *Proceedings of the 10th European Colloquium on Cytogenetics of Domestic Animals*. Utrecht: Utrecht University, 75-77.
- Forsyth Major CI. 1897.** On *Sus verrucosus*, Müller and Schlegel, and allies, from the Eastern Archipelago. *Annals and Magazine of Natural History* (6) **19**: 521-542.
- Groves C. 1981.** *Ancestors for the pigs: taxonomy and phylogeny of the genus Sus*. Technical Bulletin No. 3, Department of Prehistory, Research School of Pacific Studies, Australian National University.
- Groves CP, Grubb P. 1993.** Taxonomy and description. In: Oliver WLR, ed. *Status Survey and Conservation Action Plan: Pigs, Peccaries, and Hippos*. Gland, Switzerland: IUCN, 107-111.
- Heaney LR. 1986.** Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Zoological Journal of the Linnaean Society* **28**: 127-165.
- Heude PM. 1888.** Étude sur les Suilliens. Chapter I. *Mémoires de l'Histoire Naturelle de l'Empire Chinois*, 2, pt.3, 52-64.
- Heude PM. 1892.** Étude sur les Suilliens. Chapters III and IV. *Mémoires de l'Histoire Naturelle de l'Empire Chinois*, Vol 2, pt. 3, 212-222 and Vol 4, 113-133.
- Huet J. 1888.** Sur deux espèces nouvelles des sangliers. *Le Naturaliste* **2** (10): 5-7.
- Mohr E. 1960.** *Wilde Schweine*. Der Neue Brehm-Bücherei, no. 247. Wittenberg-Lutherstadt: Ziemsen Verlag.
- Mudar KM. 1986.** A morphometric analysis of the five subspecies of *Sus barbatus*, the Bearded Pig. MSc thesis, Michigan State University.
- Müller S. 1838.** Over eenige nieuwe zoogdieren van Borneo. *Tijdschrift over de natuurlijk Geschiedenis en Physiologie* **5**(1): 134-150.
- Nehring A. 1886.** Über zwei schädel des *Sus longirostris* Nehring von Borneo und Java. *Sitzungsberichte der Gesellschaft der naturforschende Freunde Berlin* **1886**: 80-85.
- Nehring A. 1889.** Über *Sus celebensis* und Verwandte. *Abhandlungen und Berichte der königlichen Zoologischen und Anthropologischen-Ethnographischen Museums zu Dresden*, 1888/89, **2**: 1-34.
- Nehring A. 1894.** Über Säugethiere von Philipinien. *Sitzungsberichte der Gesellschaft der naturforschende Freunde Berlin* **1894**: 179-193.
- Oliver WLR, Cox CR, Groves CP. 1993.** The Philippine Warty Pigs (*Sus philippensis* and *Sus cebifrons*). In: Oliver WLR (ed), *Status Survey and Conservation Action Plan: Pigs, Peccaries, and Hippos*. IUCN, Gland, Switzerland, 145-155.
- Sanborn CC. 1952.** Philippine Zoological Expedition 1946-47. *Fieldiana, Zoology* **33**: 89-158.
- Taylor EH. 1934.** Philippine Land Mammals. *Monograph, Philippine Bureau of Science*, no. 30. Manila, Bureau of Printing.
- Van der Made J, Han D. 1994.** Suoidea from the hominoid locality of Lufeng, Yunnan Province, China. *Proceedings, Koninklijke Akademie van Wetenschappen*, **97**: 27-82.
- Van der Made J, Moya-Sola S. 1989.** European Suinae (Artiodactyla) from the Late Miocene onwards. *Bollettino della Società Paleontologica Italiana*, **28**: 329-339.

APPENDIX

*List of specimens studied**Natural History Museum, London*

'Philippines': BM 54.3.11.7 (skin only, infant)
 Luzon: BM 97.8.4.1 (Cap Engano; skull and headskin)
 Samar: BM 86.185-7 (jaws only)
 Negros: unregistered specimens (Mt. Talinis, 9.15 N, 123.10 E; 6 skulls, 2 crania only, 5 jaws only)
 Mindanao: BM 91.11.28.3 (Ayala, type of *mindanensis*; skin and skull), 7.2.2.15 18 (Mt. Apo; skulls only)

Muséum National d'Histoire Natuelle, Paris

Palawan: MNP A.8.955-6 (Paragua, 8.58 N, 117.12 E, the second being the type of *ahaenobarbus*; skins and skulls)
 Luzon: MNP A.8.957 (Jala-Jala, Laguna Prov., type of *marchei*; skull only)

Zoologisches Museum A. Humboldt, Berlin

Palawan: ZMB 4472 (Puerto Princesa, 9.44 N, 118.42 E), 4948 (Tuitai; skull only)
 Culion: ZMB 4949 (skull only)
 Mindoro: ZMB 4886 (Calapan; skull only)
 Luzon: ZMB 4412 ('Luzon')

American Museum of Natural History (New York)

Mindanao: AMNH 242240 (Mt. Apo; skull only), 242241 (Cotabato; skull only)
 Jolo: AMNH 242242 4 (Tandulos; skulls only)

National Museum of Natural History (Smithsonian Institution), Washington, D.C.

Mindoro: USNM 113247 ('Mindoro')
 Luzon: USNM 144947 (Casiguran, mandible only)
 Leyte: USNM 458895-6 and 458901-2 (10.46 N, 124.49 E; all, jaws only), 458903 (Mt. Pangasugan, 10.46 N, 124.49 E)
 Mindanao: USNM 144718 (Datu Anibe, Catagan; jaw only), 271553 ('Mindanao')
 Negros: USNM 458904 (Dunagete, 9.15 N, 123.11 E)

Michigan State University Museum

Luzon: MSUM 34617-36 (all, Luzon, either Isabella or Cagayan Province; all, skulls only, except 34619-22 which are cranium only).

Field Museum of Natural History, Chicago

Palawan: 1151-2 (no loc., skins only); 62825 and -30 (Iwahig; skin and skull, and skull only, resp.); 62831 (skin only)
 Busuanga: 62827 (skin only)
 Mindoro: 148194 (Mayapang, Rizal, Mindoro Occidental; skull and head-skin)
 Luzon: FMNH 41889 (Manila Bay)
 Catanduanes: FMNH 142391 (cranium only), 142292-3 (jaw only)
 Masbate: FMNH 148191-2 (Conical Peak; jaws only)
 Mindanao: FMNH 56467-9 (Davao; skin only, and skins and skulls, resp.), 56474-5 (Cotabato; skin and skull, and skull only, resp.), 61018-9 (Davao; skins only), 61020-1 (Todaya; skin and skull, and skin only, resp.), 61022 ('Mindanao'), 62065-6 (Davao; skins only), 67743 (Zamboanga), 92231 (Mt. Katanglad; skin only)
 Negros: FMNH 65454-6 (Amio; skins and skulls), 66322-4 (Inubungan; skins and skulls), 66325 (Bais, Mabaha: Type of *negrinus*; skin and skull), 68001 (Iolong; skin and skull), 68002 (Santa Catalina; skin and skull), 148195 (Mt. Talinis, Negros Oriental), 148196 (Tayasan, Negros Oriental), 148198 (Patag, Silay, Negros Occidental)

Institute of Zoology (Academia Sinica), Beijing

Specimens in this collection are from the former Musée Heude, Shanghai.

They are catalogued with Heude numbers (occasionally with IZ numbers in addition) and under his taxonomic scheme, where 'N.' stands for *Nesosus*. Not all of the specific names appear to have been published.

Luzon: 1A (Manila, *N. arielinus*, cranium only), 2A-C (Jalajala, *N. effrenus*, skulls only, one with jaw), 3A (Jalajala, *N. fienatus*, cranium only), 7A-B (Jalajala, *N. minutus*, crania only), 5A (Bataan, *N. microtis*, cranium only, 8B and H1043 ('Luzon', two skulls, one with jaw).

Mindanao: 6D (Mt. Apo, 600m, *N. apoensis*, skull with jaw); 6B, 8A, 17M, 21D, 26A, 26D, 26E (all, Davao, *N. campestris*, skulls, only one with jaw); 12A = H870 (Surigao, *N. surigaensis*, subadult, skull with jaw); 72 and H857 (Mainit, *N. mamauarum*, skulls, one with jaw).

Basilan: 15B, D and F (*N. basilanensis*, subadult skulls, only one with jaw).

Tawitawi: 19A (Zoataan, *N. militaris*, cranium only).

Cebu: 4A (*N. cebifrons*, cranium only).