Taxonomy and phylogeny of the Suidae (Mammalia) in Indonesia

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Fossil and extant suids from Indonesia, ranging in age from Pliocene? to Recent, are revised. All material is ascribed to the genus *Sus*, except two species found on Sulawesi (Celebes) which belong to *Babyrousa* and *Celebochoerus*, respectively. From the ten Recent species and subspecies recognised, one from the Island of Flores – *Sus heureni* – is described as new. The Recent species are compared with the fossil ones on the basis of the same morphological characters. As a result uniformity is achieved in the classification of the extant and fossil suids. Based on this classification, the phylogeny, evolution and biostratigraphy of the various Javanese species of the genus *Sus* are discussed.

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Introduction

The Suidae are one of the most successful families within the order of the Artiodactyla and they are distributed over Africa and Eurasia. In Indonesia (Fig. 1) suids are known from Pliocene?, Pleistocene and Holocene deposits and are represented mainly by the genus *Sus*. It is only from Sulawesi that two other genera have been reported: *Babyrousa* and *Celebochoerus*, the latter being extinct. Recent suid species in Indonesia are: *Sus scrofa (Sus vittatus), Sus barbatus, Sus verrucosus, Sus celebensis,* and *Babyrousa babyrussa*. Three other species – *Sus floresianus, Sus timorensis* and *Sus papuensis* – are also described but their validity is under discussion. There is no consensus of opinion about the taxonomy of the Recent species of Sus in Indonesia.

Little is known about the origin, migrations and evolution of the species of the genus *Sus*. So far there have been very few publications about extant and fossil suids from Indonesia. One of the purposes of this study is to obtain a better understanding of the phylogeny of Suidae, especially those of Java.

The palaeontologist and the zoologist apply a different methodology to distinguish the different species. The zoologist bases his description of the extant species on the external morphology, especially on the skull structure, the skin and the hair, but pays little attention to the teeth. The palaeontologist on the other hand uses teeth for his taxonomy. Needless to say, it is difficult to match the taxonomy of the fossil suids with that of the extant suids from Indonesia. If one wants to study the relation between the living pigs and the fossil ones, it would seem that a different approach is required.

The first task is to study the size and morpholgy of those parts of the Recent material which can also be found as fossils: skull, teeth, foot bones, etc. The second task is to find out what variation there is within a species. Therefore an attempt has to be made to find a sample from one level at one locality which we can assume to be a sample of one species, or better of one population. Such a sample can be used as a standard. If we know the variation within that standard population or species, then we can compare this sample with other samples from other localities and then we can also deduce whether these fit into the range of the determined species.

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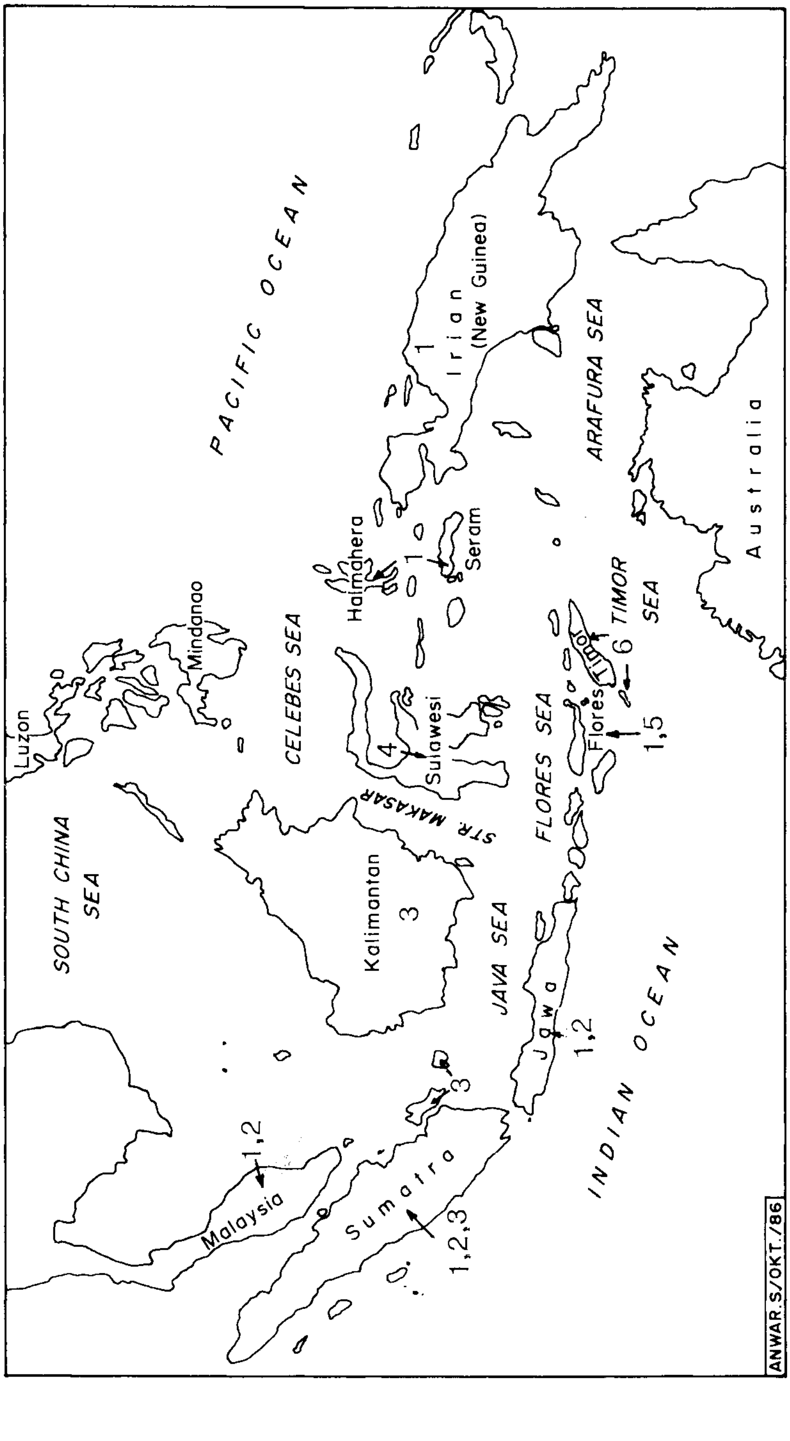

Fig. 1. Map of Southeast Asia, showing Indonesia and adjacent countries. The Recent distribution of the various *Sus* species in Indonesia is shown by the numbers in this figure.
1 – *Sus scrofa* Linnaeus, 1758; 2 – *Sus verrucosus* Müller & Schlegel, 1845; 3 – *Sus barbatus* Müller, 1838; 4 – *Sus celebensis* Müller & Schlegel, 1845; 5 – *Sus heureni* sp. nov.; 6 – *Sus timorensis* Müller & Schlegel, 1845.

Senckenberg Museum, Frankfurt (West Germany); Dr P.J.H. van Bree, Zoological Museum, University of Amsterdam, Amsterdam (The Netherlands); Dr G.J. Bartstra, Biological-Archaeological Institute, of Groningen (The Netherlands); Dr V. Eisenmann, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris (France); Drs J.J. Hoocker and A.W. Gentry, British Museum of Natural History, London (England); Dr D. Kader, Mr F. Aziz and Mr Suwarno, Geological Survey of Indonesia, Bandung (Indonesia); Mr Buadi, Zoological Museum, Bogor (Indonesia).

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METHODOLOGY

Studied material

The Recent material studied is stored in the Rijksmuseum van Natuurlijke Historie (National Museum of Natural History, Leiden: RMNH), in the Zoological Museum of the University of Amsterdam (ZMA) and in the Bogor Zoological Museum. The fossil material studied comes from the Dubois Collection, RMNH; Department of Geology, Bandung Institute of Technology; the Geological Survey, Bandung; Institute for Earth Sciences, University of Utrecht; and from the Senckenberg Museum.

Linear measurements

The measurements are taken with sliding calipers, accuracy to 0.1 mm. The calipers used are of a 150 mm and a 500 mm size. All measurements are expressed in millimeters unless otherwise indicated. The measurements shown in the figures are taken partly from von den Driesch (1976). Morphology and supplementary measurements will be indicated in the text.

Terminology

The nomenclature for the skull morpholgy (Figs. 2-6) is based mainly on Sisson and Grossman (1953), that of the snout region on Harris and White (1979). The (horizontal) axis of the skull is an imaginary line, starting at the mid anterior part of the praemaxilla running to the mid base of the foramen magnum. The vertical axis of the skull is perpendicular to this horizontal axis.

For the description of the teeth the Cope/Osborn terminology is used in a topographical way. The molar morpholgy (Figs. 7-8) is described according to Wilkinson (1976). The praemolar cusps are described according to their position.

Standard for comparison

The suid collection from Trinil will be used as a standard for comparing the various fossil assemblages from Java.

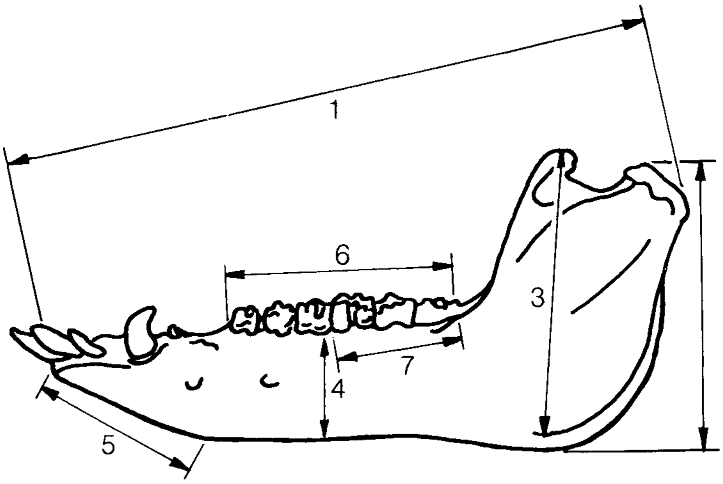


Fig. 2. Left lower jaw of *Sus*: 1 – length of lower jaw; 2 – height of lower jaw; 3 – height of coronoid; 4 – height of ramus; 5 – length of symphysis; 6 – length of P_2-M_3; 7 – length of M_1-M_3.

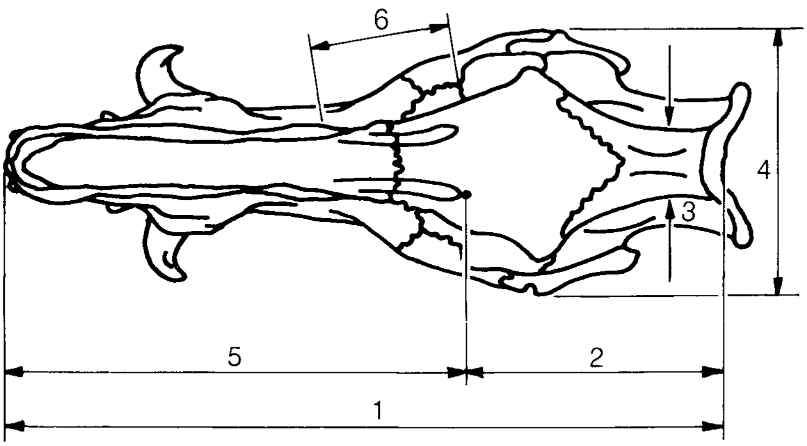


Fig. 3. Dorsal view of *Sus* skull: 1 – length of skull: tip of praemaxilla to back of occipital crest; 2 – length of hind part of skull: point between supraorbital foramina to back of occipital; 3 – width of parietal crest; 4 – bizygomatic width; 5 – length of rostrum: tip of praemaxilla to the point between supraorbital foramina; 6 – lacrimal-infralacrimal length.

Diagram of the mean dimension of the skull and the lower jaw of Sus

The diagrams showing the mean dimensions of the skull and the lower jaw were constructed according to Eisenmann (1979). The values plotted on the diagrams are the logarithmic differences between the mean dimension of the various characters of the species studied and those of the standard species.

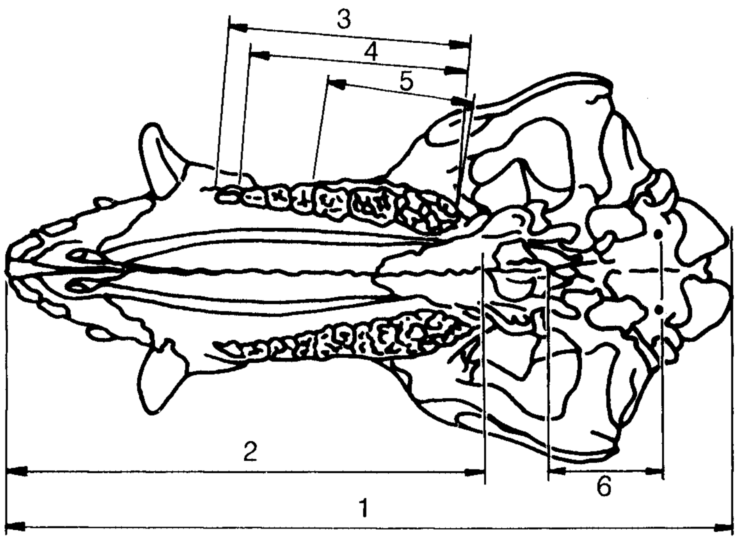


Fig. 4. Ventral view of *Sus* skull: 1 – condylo-basal length; 2 – length of palatine; 3 – length of P^1-M^3; 4 – length of P^2-M^3; 5 – length of M^1-M^3; 6 – length of basioccipitoparasphenoid.

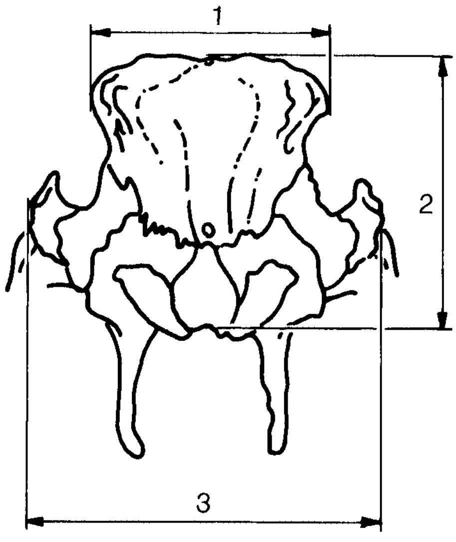


Fig. 5. Posterior view of *Sus* skull: 1 – width of occipital crest; 2 – occipital height; 3 – temporal width.

The scrofic and the verrucosic groups

Stehlin (1899) differentiated the scrofic and verrucosic groups on the basis of the outline of the cross-section of the male lower canine (see Fig. 9). In the scrofic type the posterior side of the canine is broader than the buccal side; in the verrucosic type the posterior side

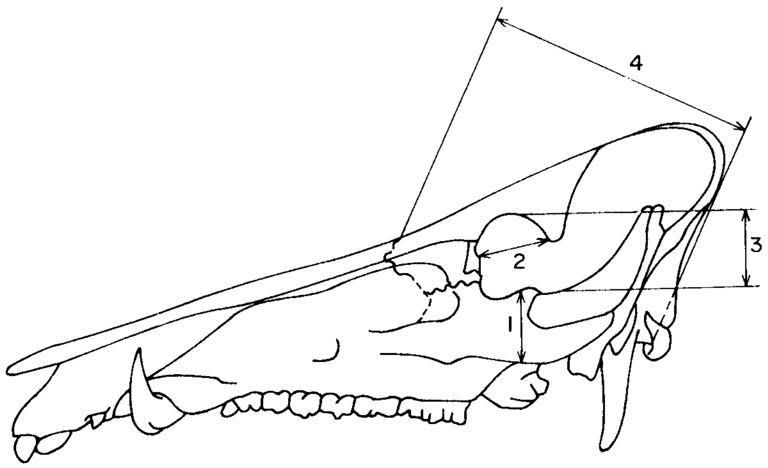


Fig. 6. Lateral view of *Sus* skull: 1 – width of jugal; 2 – width of orbita; 3 – height of orbita; 4 – distance between posterior nasal and foramen magnum.

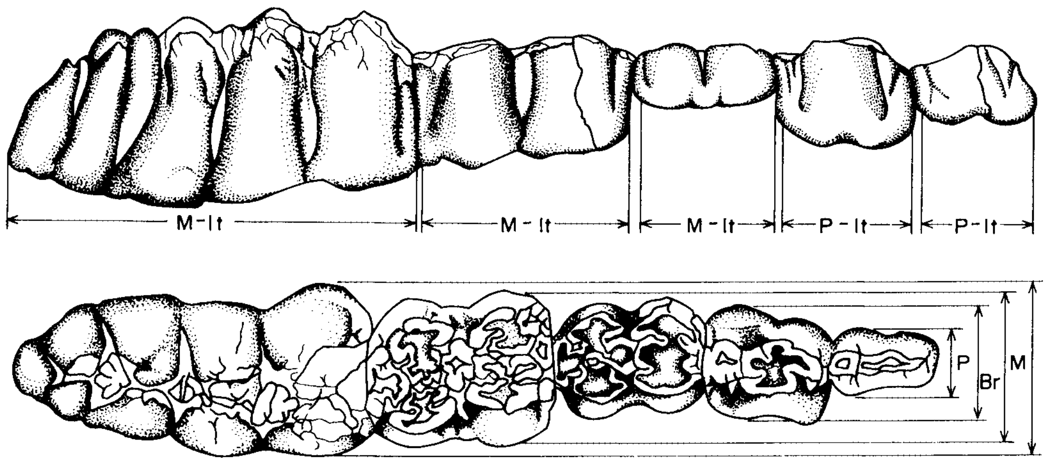


Fig. 7. Measurements of the lower molars and praemolars of *Sus*: M-lt – length of molar; P-lt – length of praemolar; Ht – height of molar; M – width of molar; P – width of praemolar; Br – width of M_2.

is narrower. On the basis of the characters of the female lower canine no differentiation is possible. The other characters which can be used as criteria to differentiate the two groups, regardless of the sexes of the specimens, are the stylus and the stylid of the second and the third upper and lower praemolars. In the verrucosic group, they are more strongly developed than the stylus and the stylid of the same teeth in the scrofic group.

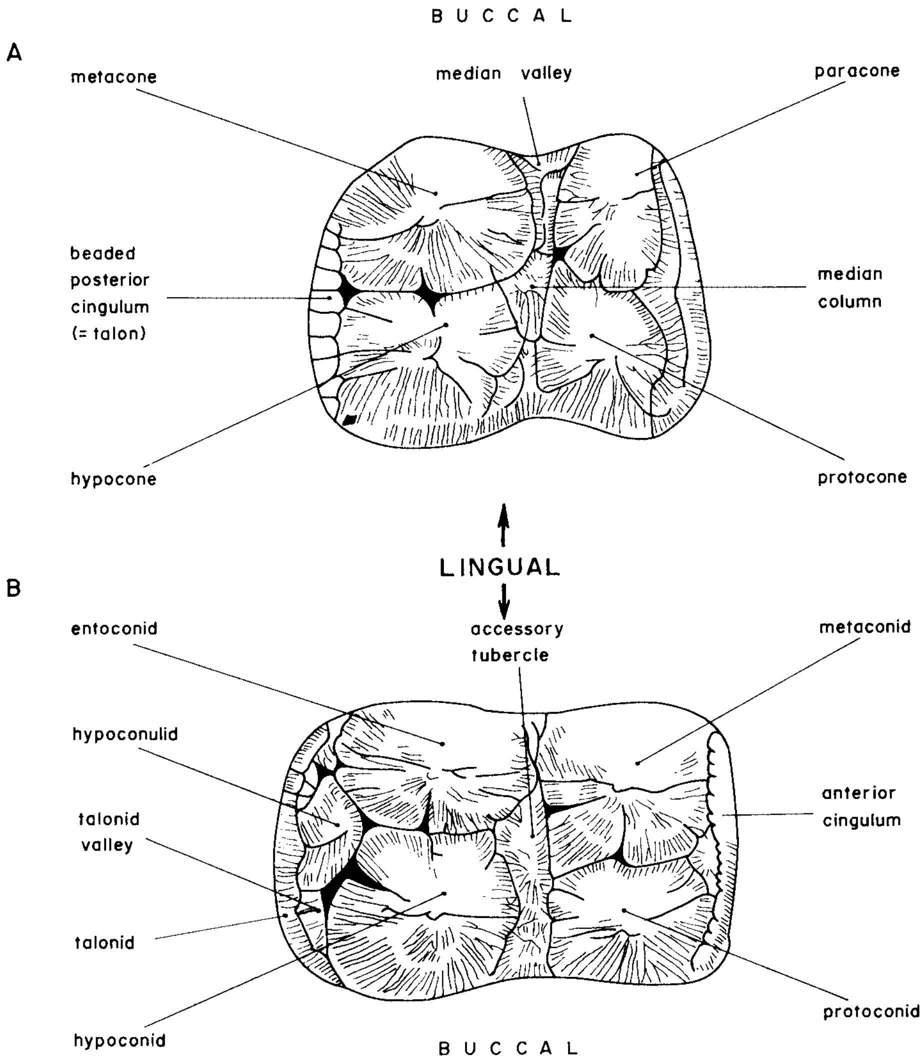


Fig. 8. Nomenclature used in tooth descriptions. In both cases the anterior side of the tooth is to the right, the posterior side to the left. A: M^2 dext.; B: M_2 dext.

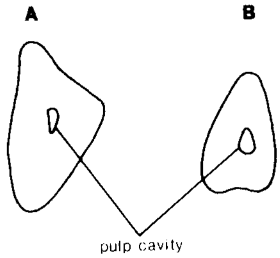


Fig. 9. Cross section of two types of male lower canines of suids; in both cases, front edge of tooth above; buccal side to the right. A – scrofic group; B – verrucosic group.

REVIEW OF THE LITERATURE

Fossil suids have been described from Java and Sulawesi (Figs. 10-11). However, the accompanying fossil faunas of both islands are different: on Java the fauna is balanced, whereas the fauna of Sulawesi is endemic, impoverished and without carnivores. A historical review of the literature concerning the pigs from the two islands will therefore be presented separately.

Java

Already in the 19th century vertebrate fossils have been recorded from Indonesia. Junghuhn (1857) was apparently the first person to report on fossils from Patiayam. Raden Saleh (1867) reported the presence of fossils at Gunung Pandan and Sentolo near Yogyakarta.

Fossil suids were mentioned by Martin (1890). In a list of the fossil fauna from Java he included *Sus hysudricus*, which was referred to *Sus brachygnathus* by Dubois (1891, nomen nudum).

Dubois (1891) wrote on the vertebrate fossils from Pleistocene and Tertiary deposits on Java (collected in 1890), and mentioned suids from Gunung Kendeng, Patiayam and some other places in Central Java. He provisionally identified the suids from the Kendeng localities as *Sus celebensis, Sus verrucosus?* and *Sus vittatus?* Later Dubois (1908) reported on the fauna from the Kendeng deposits and he identified two pig species: *Sus brachygnathus*, which is comparable to the Recent pig *Sus celebensis* from Sulawesi (Celebes), and *Sus macrognathus*, which is comparable to Recent pig *Sus verrucosus* Müller from Java. However, Dubois did not give adequate descriptions, measurements or accompanying figures, nor did he designate a type species. Dubois (1908) also wrote that *Sus hysudricus*, mentioned by Martin (1890), was the same species as his *Sus brachygnathus*.

Stremme (1911) described fossils from Trinil near Ngawi in East Java. For the pigs, Stremme (1911) used the names given by Dubois (1908). *Sus brachygnathus* and *Sus macrognathus* have become better known since Stremme's publication.

Most of the suid fossils from Java came from Central and East Java, very few from West Java. The fossil suids from West Java were reported for the first time by Stehn and Umbgrove (1929, p. 6, pl. 4, fig. 4). The fossils they mentioned were collected from lacustral strata in the western part of the Bandung highlands near a place called Batujajar. Other fossils found there were *Bos* and *Cervus*. They identified the suid fossils as *Sus brachygnathus*, but the dimensions are too large for that species. Four years later these fossils were identified by von Koenigswald as *Sus terhaari*. Later von Koenigswald (1935) also reported the fossil *Sus* sp. from the Tambakan Beds near Subang (West Java) (Fig. 10). According to von Koenigswald *Sus* fossils were very scarce in those localities.

Von Koenigswald (1933) listed and described more suids from Java. His list contains seven species: *Sus brachygnathus* Dubois, *Sus macrognathus* (Dubois) Stremme, *Sus* ex. aff. *vittatus* Temm., *Sus stremmi* sp. nov., *Sus vatualangensis* sp. nov., *Sus terhaari* sp. nov., and *Sus* sp. He compared these species with the Recent species, *Sus celebensis, Sus verrucosus, Sus barbatus,* and *Sus vittatus*. Von Koenigswald followed Stehlin (1899) in dividing the suids of Indonesia into two groups, a *verrucosus-celebensis* and a *scrofa-vittatus* group; this division is based on the cross section of the male lower canine.

Badoux (1959) discussed the validity of Dubois' species, *Sus brachygnathus* and *Sus macrognathus*. After making some comparisons and an analysis based only on the

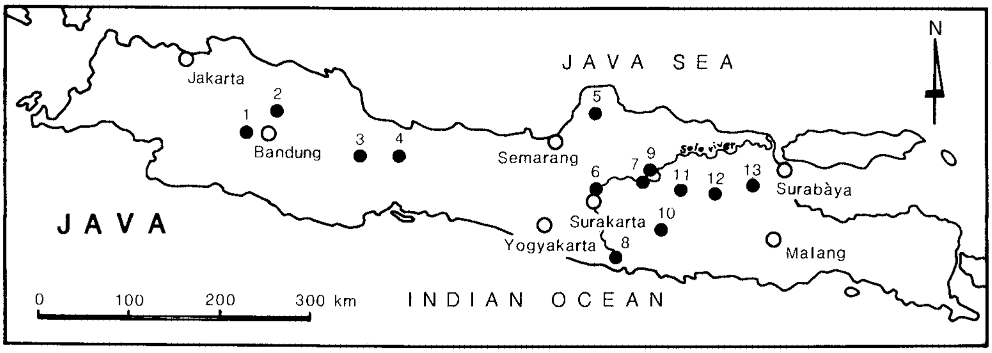


Fig. 10. Sketch map showing fossil vertebrate localities on Java.
1 – Batujajar; 2 – Tambakan; 3 – Cijulang; 4 – Bumiayu; 5 –Patiayam; 6 – Sangiran; 7 – Trinil; 8 – Punung; 9 – Ngandong; 10 – Sampung; 11 – Kedungbrubus; 12 – Bangle; 13 – Mojokerto.

teeth, he came to the conclusion that *Sus brachygnathus* was a synonym of *Sus verrucosus*. In Badoux's views von Koenigswald's species *Sus terhaari* was a specialised *Sus verrucosus*, and should be called *Sus verrucosus terhaari*.

In 1963 von Koenigswald published another article on the suids of Java in which he described relatively small teeth from Sangiran (Central Java). After taking some measurements and comparing them with measurements of all the known species from Java, he came to the conclusion that the small teeth, and M_3 and P^4, belong to the new species *Sus sangiranensis*. According to von Koenigswald (1934) the new species came from the Jetis beds at Sangiran.

Sulawesi (Celebes)

The first fossil pigs from Sulawesi described in a publication (Hooijer, 1948) were specimens of a large suid collected by van Heekeren at Desa Beru and Sompoh. Sompoh is situated 12 km north of Beru, near Kecamatan Soppeng, between the Wallanae River and the Singkang depression, about 100 km northeast of Ujungpandang in South Sulawesi. According to Hooijer (1948) the exact stratigraphical position of the specimens is uncertain, but he suspected the age of the layer from which they originated to be latest Middle Pleistocene or Late Pleistocene. Hooijer (1948) assigned these suid fossils to a new genus and a new species, *Celebochoerus heekereni*. Other fossils in the collection were *Babyrousa, Anoa,* a small *Archidiskodon,* and a tortoise (*Geochelone*).

Hooijer (1948, p. 1025) diagnosed his new genus as follows: 'A giant suid with upper canines subtriangular in cross section and only slightly constricted at the pulp cavity...' The diagnosis of the type species, *Celebochoerus heekereni*, is the same as the generic one. The holotype is the base of an upper canine; the paratype is a portion of a right upper canine. The type-locality is Desa Beru, Cabenge, which is Pleistocene in age. Hooijer (1948) presented a plate, with six figures. In his paper (1948) Hooijer compared his *Celebochoerus* with the African *Potamochoerus* and with other *Sus* species.

Furthermore Hooijer (1948) established a new subspecies of *Babyrousa babyrussa*, and called it *Babyrousa babyrussa beruensis*. The type specimen of this new subspecies was also collected by van Heekeren. Hooijer (1948) reported that the fossil belonged to the Recent species, but was larger. He compared the M_3 of the fossil subspecies with the Recent subspecies *Babyrousa babyrussa babyrussa* from Buru and Sulawesi, but he did

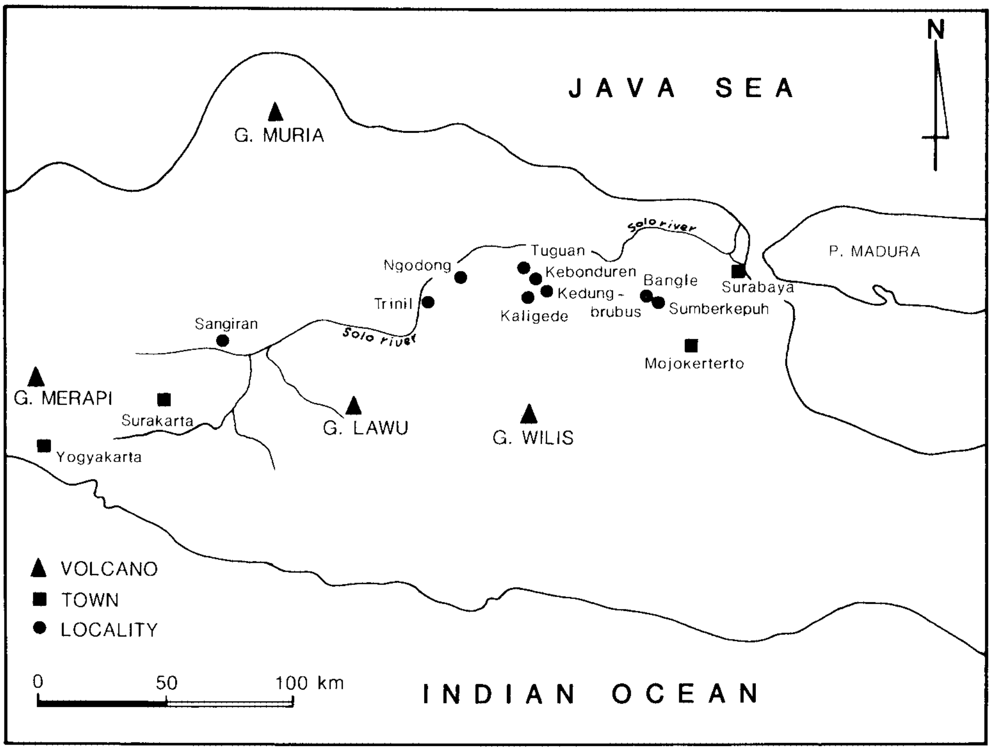


Fig. 11. Sketch map of Central and East Java showing localities with *Sus* fossils.

not compare it with *Celebochoerus heekereni* which came from the same deposit. In 1950 and 1954 Hooijer reported additional material of *Celebochoerus*. The following specimens are described: part of a right upper canine (11 cm in length, from Sompoh, the most complete specimen at that time) and a right canine (equally from Sompoh and measuring 23 cm). Their cross-sections are alike. The upper longitudinal groove is situated closer to the middle of the upper surface. The newly acquired canines consequently show that the Pleistocene suid of Sulawesi had upper canines with the enamel stripe restricted to the central surface. No enamel ridges occur on the anterior and posterior upper edges of the canine, which is opposed to what is commonly found in *Sus*.

A fossil specimen belonging to the extant species *Sus celebensis* was described by Hooijer (1969). The specimen was collected by N. Adrian from the bed of the River Salo Paciro between Pampanua and Soppeng, South Sulawesi. This fossil was passed on to the Zoological Museum of Amsterdam in 1932. It consists of the palate with P^3, M^3 on the left side and P^4-M^3 on the right side. The M^3 is still present in the alveole and its anterior part is not even slightly worn. According to Hooijer (1969) this specimen undoubtedly belongs to *Sus* and there are no morphological differences between the fossil specimen and the extant species *Sus celebensis*. On the measurements of fossil, subfossil and Recent specimens Hooijer (1969) concluded that the teeth of *Sus celebensis* have increased in size since the Pleistocene.

In 1972 Hooijer described more remains from the giant fossil pig, *Celebochoerus heekereni*, and reported that *Celebochoerus* was the most common fossil in this area.

From Calio he described an almost complete palatum and the distal end of a radius; from Sompoh he reported a proximal dextral humerus and from Beru a first phalanx.

Clason (1976) reported on the excavation in the Ulu Leang region, where there are many caves, calling the area Ulu Leang I. The pottery and other remains were dated by means of the ^{14}C method and she reported an age of c. 5000-6000 years B.C. Quoting a publication of Glover and Highan, she stated that the domestic pig and goat had been introduced onto Timor and the highlands of New Guinea between 2000 and 3000 years B.C. She presumed that the domestic pig was introduced to Sulawesi even earlier (6000-8000 years B.C.). In one cave, Clason (1976) identified two suid forms *Sus verrucosus* and *Babyrousa babyrussa*, the former also being called *Sus celebensis*. According to Clason (1976) it is possible to differentiate between the species only on the basis of the dental elements. In this publication she recalls the similarity between the Celebes pig and the European pig and also comments on some ecological features of the Sulawesi pig. She stated that in the Ulu Leang caves the pig remains are numerous. In her opinion a third species, *Sus scrofa* (domesticated), was present as well. The *Sus scrofa*, she mentioned, must have come to Sulawesi earlier than to New Guinea.

Historical review of the Recent species

The first record of Indonesian suids appeared in Linnaeus' Systema Naturae, 10th edition (1758). The suid he mentioned was *Sus babyrussa* Linnaeus. He gave the type locality as Borneo (= Kalimantan), but he should have written Buru (see Ellerman & Morrison-Scott, 1951). Müller and Schlegel (1845) described five species of wild boar from Java, Sumatra, Kalimantan, Sulawesi, and Timor: *Sus barbatus, Sus verrucosus, Sus vittatus, Sus celebensis,* and *Sus timorensis*. *Sus celebensis* was considered a subspecies of *Sus verrucosus* by Ellerman & Morrison-Scott (1951) and Laurie & Hill (1954) referred to it as *Sus scrofa timorensis*, which is basically incorrect, because *Sus timorensis* belongs to the *verrucosus* group and not to the *scrofa* group.

Flower and Lydekker (1891) described two groups of Indonesian pigs in the genus *Sus*, viz. the *scrofa-vittatus* and the *verrucosus-celebensis* group, but did not explain the difference between the two groups. Stehlin (1899) was the first to characterise both groups on the basis of the morphology of the male lower canine.

Jentink (1905) accepted all the Müller and Schlegel species and added four new species, viz. *Sus milleri, Sus nehringii, Sus weberi,* and *Sus floresianus*. In his monograph, he wrote that he did not believe Major (1897) who reported the species *Sus verrucosus* from Kalimantan. According to Jentink this species did not occur there.

Chasen (1940) listed all the mammals from the Sunda Islands, in which he included Java, Sumatra, Kalimantan, and the Malay Peninsula, using the old nomenclature. His publication was supplemented by Ellerman & Morrison-Scott (1955) who followed the new nomenclature and assigned *Sus vittatus* and *Sus milleri* as subspecies to *Sus scrofa*.

Sody (1941) pointed out that there could have been different races of pigs in the Lesser Sunda Islands. He thought that many of the *Sus* species described by previous authors, especially those of the *scrofa-vittatus* group, were not valid species. He suggested that those species should be considered subspecies of *Sus vittatus*. His idea was later followed by Ellerman & Morrison-Scott (1951, 1955), who concluded that 'The pigs of the Lesser Sunda Islands are subspecies of *Sus scrofa*'. Hoogerwerf (1970) wrote about the wild boar of Ujungkulon, Java. According to him *Sus verrucosus* and *Sus scrofa milleri* live in the Ujungkulon nature reserve. Concerning the geographical distribution he stated that *Sus verrucosus* is also present in Kalimantan; many authors do not agree with him about this.

Groves (1976) considered the wild pig on Sulawesi a separate species, *Sus celebensis*. Lord Medway (1977) does not seem to agree with Major (Jentink, 1905) and Hoogerwerf (1970) about the distribution of *Sus verrucosus*. He recognised only one species on the Island of Kalimantan: *Sus barbatus*.

Groves (1980) revised the genus *Babyrousa* present on Kalimantan, Buru and the adjacent islands. According to him the *Babyrousa* in Central Sulawesi is morphologically very close to the type species from the Island of Buru. Groves (1981) discussed the genus *Sus* and its various subspecies. According to him the pigs on New Guinea and the adjacent islands are the result of hybridization between *Sus celebensis* and *S. scrofa*. However, this is very unlikely because it is known from Sumatra and Java that there is no interbreeding between: *Sus scrofa* (scrofic group) and species of the verrucosic group (Hoogerwerf, 1970).

Taxonomy

DESCRIPTION OF THE FOSSIL MATERIAL

Introduction

It has been mentioned before that the taxonomy of the fossil pigs of the genus *Sus* in Indonesia is confused. Von Koenigswald (1933) accepted seven species and Badoux (1959) put them all in the two extant species. A recent publication by de Vos et al. (1982) shows that various faunas can be distinguished within the Pleistocene. The differences are due to differences in age of the localities. Since the fossil pigs of Java found so far all belong to the genus *Sus* and the main differences so far described are differences in the size of some teeth, it is necessary to treat the material locality by locality. From this we may find out if there are differences in the fossil pigs too, as has been demonstrated for the other faunal elements. De Vos et al. (1982) showed that Trinil has a special faunal association and suggested that this fauna is older in age than that of Kedungbrubus; *Sus* is present in both faunas.

The locality of Trinil (Trinil s.s) is quite homogeneous in its faunal composition, as was shown by two excavation campaigns: by Dubois from 1890 to 1900 and by Selenka in 1907 and 1908. From his collection Dubois (1908), described the new species *Sus brachygnathus*, but he did not figure a specimen nor did he designate a holotype. Stremme (1911) described the species in more detail and figured material, but he did not designate a holotype either. According to de Vos et al. (1982) the Trinil material was excavated by Dubois from one lithostratigraphical level and represents one age. On that basis we can consider the Trinil pig fossils as an homogeneous sample, which can be used as a standard for comparison. Since the original author did not designate a holotype for *Sus brachygnathus*, a lectotype will be chosen from the material on which Dubois based his species.

Dubois (1908) also described *Sus macrognathus*, without giving the locality of provenance. Stremme (1911) too described and figured the species using material from Kedungbrubus. The species names *Sus macrognathus* and *Sus brachygnathus* are widely used with a uniform meaning. In order to validate this usage, a lectotype will also be chosen for *Sus macrognathus* from the material in the Dubois collection from the locality Kedungbrubus.

Systematics

Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821
Genus *Sus* Linnaeus, 1758

Sus brachygnathus Dubois, 1908
Pls 1-3, Table 1.

Sus hysudricus Martin, 1890.
Sus celebensis Dubois, 1907, nomen nudum.
Sus brachygnathus Dubois, 1908.
Sus macrognathus Stremme, 1911, part.
Sus vatualangensis von Koenigswald, 1933.
Sus barbatus, Badoux, 1959.

Lectotype — A lower jaw, left and right, coll. Dub. 1861, Pl. 1, figs. B, D.

Type-locality — Trinil s.s., near Ngawi, East Java.

Type-horizon — Hauptknochenschicht (Carthaus, 1911), Pleistocene.

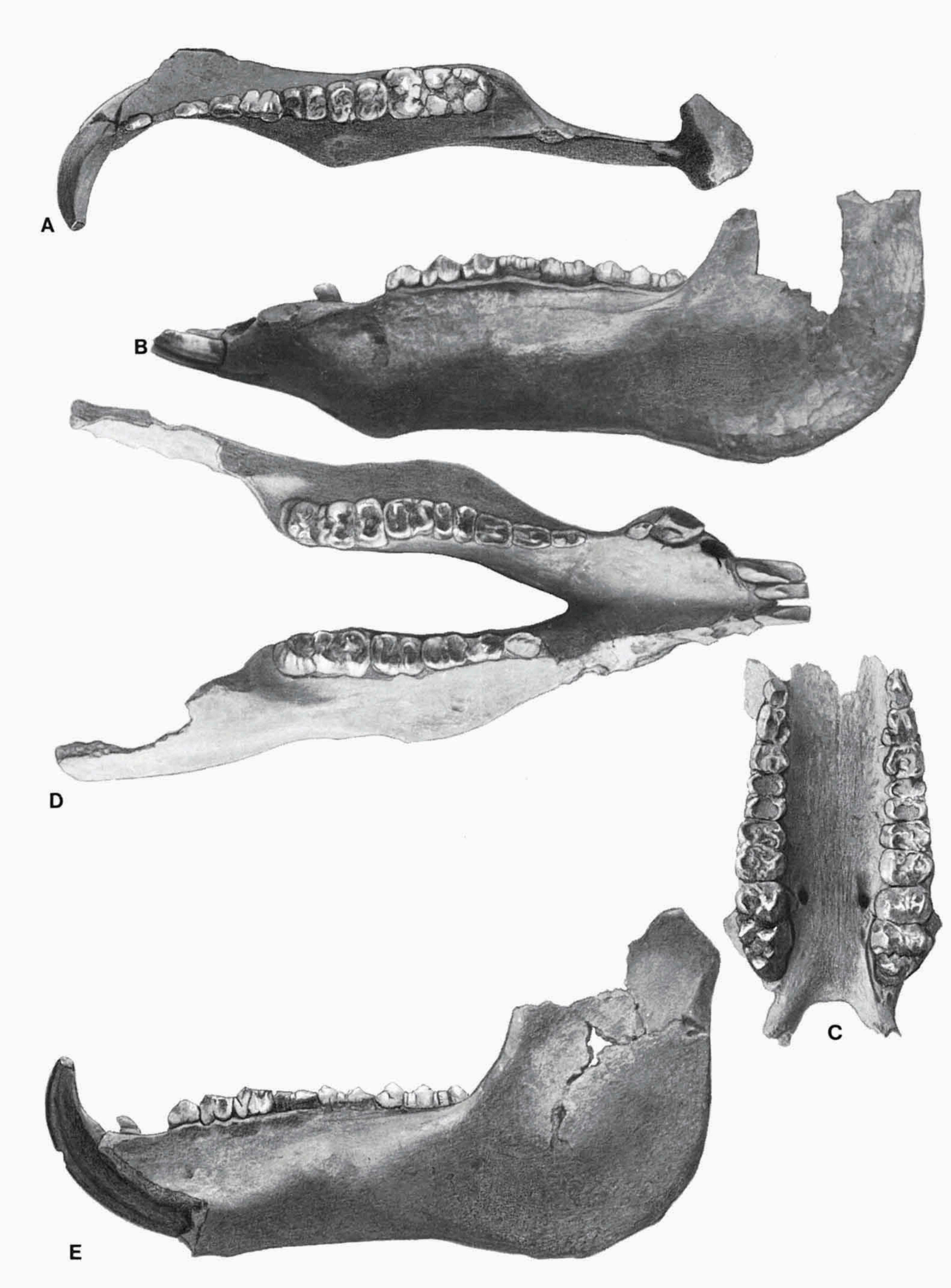
Diagnosis — Small pig from Java, but larger than the smallest pig (*Sus sangiranensis* von Koenigswald, 1963). The male lower canine is of the verrucosic type. The P_3 is smaller than the ones in *Sus verrucosus* and its talonid is less complicated. The anterior buccal stylus of the P^2 and P^3 is more prominent. The zygomatic arch is narrower and less inflated than it is in *Sus verrucosus*. Compared to the latter species the orbit is relatively large and the zygomatic maxillary or facial crest, which divides the fossa for the insertion of the levator nasalis muscle and that for the insertion of the depressor nasalis, is much more pronounced. Both depressions are more deeply scooped out than in *Sus verrucosus*. The edge of the dorsal surface of the frontal bone is less rounded and forms a sharp edge.

Description — The length of M_3 is 32.4 mm and its width is 16.9 mm. The length of M_1 plus M_2 is about equal to the length of M_3. The ramus of the lower jaw is inflated.

Symphysial part — The symphysis is of moderate size, extending posteriorly to the second praemolar. The external surface descends gradually to under the anterior canine alveole. From this point it goes down more steeply to the end of the symphysis. There is a marked post-canine constriction between P_1 and P_2, but closer to P_1. Maximum expansion of symphysis occurs at the canine alveole just at the corner of the rear and the outer flank of the canine alveole. The symphysis narrows in front of the canine. There is a depression, which is V-shaped in cross section, between left and right canine. The mental prominence is fairly developed.

Ramus — The ramus is relatively short and thick. The lateral inflation is markedly pronounced laterally. The maximum inflation occurs under the M_1. There is an extramolar shelf outside (buccal side), but there is no intramolar shelf (lingual side). The mental foramen is in the front part at the edge of the symphysis. There is a deep, clear depression inside the ramus, under the mental bullae, starting under the M_3. In this specimen the coronoid and the condyle are missing. The inner surface of the gonion caudale and ventrale is irregularly undulating. The jaw muscle is attached to this structure. The central part of the ramus is also missing.

Plate 1



Sus brachygnathus Dubois, 1908
Trinil s.s.
Fig. A. Left lower jaw, coll. Dub. 1848, top view, approx. × 0.38.
Fig. B. Lower jaw, lectotype, coll. Dub. 1861, lateral view, approx. × 0.33.
Fig. C. Palatine with upper jaw dentition, coll. Dub. 1846, approx. × 0.55.
Fig. D. Lower jaw, lectotype, coll. Dub. 1861, top view, approx. × 0.33.
Fig. E. Left lower jaw, coll. Dub. 1848, lateral view, approx. × 0.41.

Dentition

Incisors — I_3 is missing, leaving only an alveole. I_2 is longer than I_1, the lingual side is abraded.

Canine — The canine is of the verrucosic type (posterior surface narrower than the buccal surface). In this specimen the occlusal parts are missing, as the teeth are broken off at the alveole.

Praemolars — P_1 is small, with a single lobe. The edge is corrugated; lingual and buccal walls are slightly convex. The wear edge runs obliquely backwards. There is a diastema of 14.5 mm between P_1 and P_2. P_2 consists also of a single lobe. The anterior and posterior surfaces are worn. At the base, on the anterior and posterior sides, small stylids are present. Cusps are not distinctly developed but the surface is somewhat corrugated. P_3 is larger than P_2. The stylids on the buccal side are more pronounced in that they show an anterior and a posterior constriction. On the lingual side the stylid is less developed. The longitudinal ridges of P_2 and P_3 are in line. The logitudinal ridge on the P_4 is also more or less in one line with those of the preceding praemolars. The posterior part of the ridge shows a minor small cusp at the buccal side, and the anterior stylid is also prominent, as a result of which the P_4 shows a molarisation tendency. On the lingual side the stylid is weakly developed.

Molars — M_1 is rectangular. The tooth is worn, showing the dentine. A small accessory cusp is situated on the buccal side of the median valley. The molars are smaller than those of *Sus verrucosus*. M_2 has a more or less rectangular shape too. The accessory cusp in the median valley is larger than that of M_1. The hypoconulid is developed as a posterior ridge. M_3 is longer than M_2. The talonid is well developed. This molar is narrower than the corresponding one of *Sus verrucosus*. The median column is developed in the median valley, and the hypoconulid column in the talonid valley, buccal to the hypoconulid; both are clearly visible. There is also an accessory cusp on the lingual side of the tooth, which is connected with the hypoconulid. The talonid consists of one pair of cusps and a terminal cusp. The latter is divided by a shallow groove. The talonid of the third molar of *Sus brachygnathus* is less complex than that of *Sus verrucosus*. The dentition of the right lower jaw varies in minor details only from the left one.

Paratype 1 — A palatine, coll. Dub. 1846, Pl. 1, fig. C.

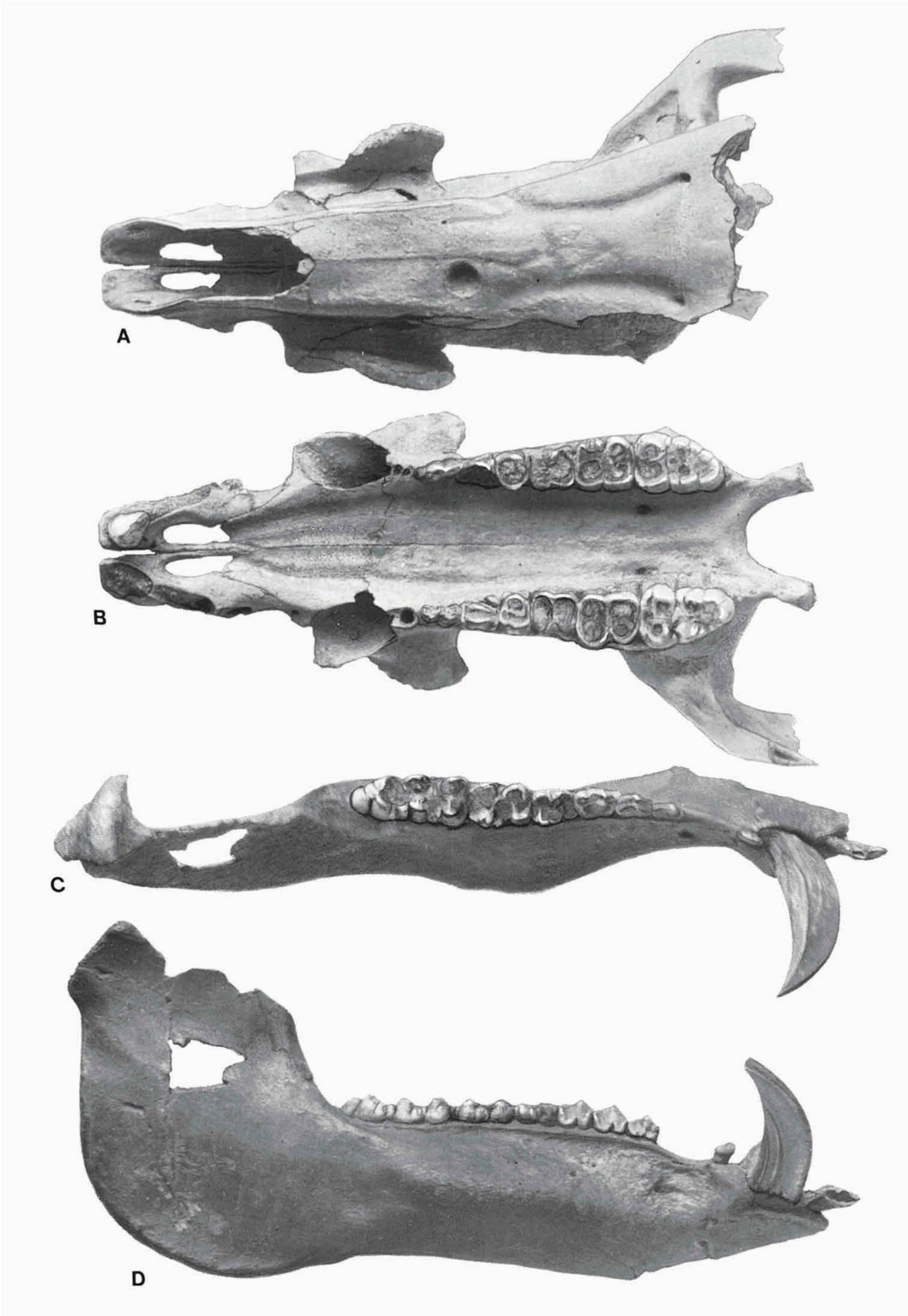
Locality — Trinil s.s.

Description — Palatine with upper dentition; both sides, with P^2-M^3. The antero-buccal corner of left M^1 is broken off, otherwise the dentition is well preserved. Laterally the maxilla is open, showing the roots of the cheek teeth. P^3, canine and incisor are missing. On the right side, above P^3 and P^2 a trace of the maxillary process is visible, which is part of the canine flange wing. The nasal sinus opens dorsally. In the posterior part, the U-shaped palato-nasal border is clearly visible. Between the left and right side third molars a pair of palatine foramina is present. The palatine groove, starting from the front of the palatine foramen, is only weakly developed.

Dentition — The incisors, canines and first praemolars are missing on both sides. The description is based on the dental elements of the left side.

Syntype 1 — A female skull, coll. Dub. 1862, Pl. 3.

Plate 2



Sus brachygnathus Dubois, 1908
Trinil s.s.
Fig. A. Skull of adult male, coll. Dub. 1860, dorsal view, approx. × 0.36.
Fig. B. Idem, ventral view, approx. × 0.36.
Fig. C. Right lower jaw of adult male, coll. Dub. 1854, top view, approx. × 0.49.
Fig. D. Idem, lateral view, approx. × 0.49.

Locality — Trinil s.s.

Description — The right zygomatic arch is relatively well preserved even though its upper part is missing. The lower part of the occipital bone as well as the left occipital condyle are well preserved. The right temporal region is better preserved than the left-side region. Basioccipital and the basihyoid are missing, but both auditory bullae are well preserved. Only the base of the two vertical processes of the skull is left. The palatine bone is in good condition. The skull is elongated and pointed, with an almost straight profile from the nasal to the parietal bone. The brain case is domed behind the orbit. Judging from the position of the parietal crest the parietal constriction was probably narrow. The specimen also has a relatively long snout which resembles that of *Sus verrucosus* but is smaller. Its dorsal surface is flat and the lateral borders of the nasalia are parallel. The zygomatic arch is less inflated than in the male specimen (coll. Dub. 1860). The width of the maxillary part of the zygomatic arch is narrower in the female *Sus verrucosus*. The malar part of the zygomatic arch is thin. The surface of the temporal bone is almost vertical and the temporal bone is almost vertical and the temporal condyle is in an almost horizontal plane. The lower side of the temporal fossa is convex anteriorly but concave posteriorly in order to accommodate the condyle of the lower jaw. The upper part of the foramen magnum has a triangular opening on the left side. The external auditory opening has a relatively lower position than that in *Sus verrucosus*. The orbit is relatively large and the supra-orbital process is not connected to the zygomatic process of the maxillary. The auditory bullae are compressed laterally and are situated in front of the vertical processes (= paroccipital process). The palatine bone has two palatine foramina and two grooves start from these foramina, running posteriorly.

Dentition — The dentition resembles that of the paratype, except for P^1 sin. The latter shows three small conules or accessory cusps.

Incisors — I^1 is large, flat and slightly curved inside and downwards. I^2 and I^3 are spatulate and have three cusps. I^2 has an accessory cusp on the postero-lingual side.

Canine — The canine is small. Its shape resembles that of the extant species, being spatulate. Its position in the skull is such that its apex is directed downwards. The rest of the dentition is the same as that of paratype 1.

Syntype 2 — Right lower jaw, coll. Dub. 1854, Pl. 2, figs. C, D.

Locality — Trinil s.s.

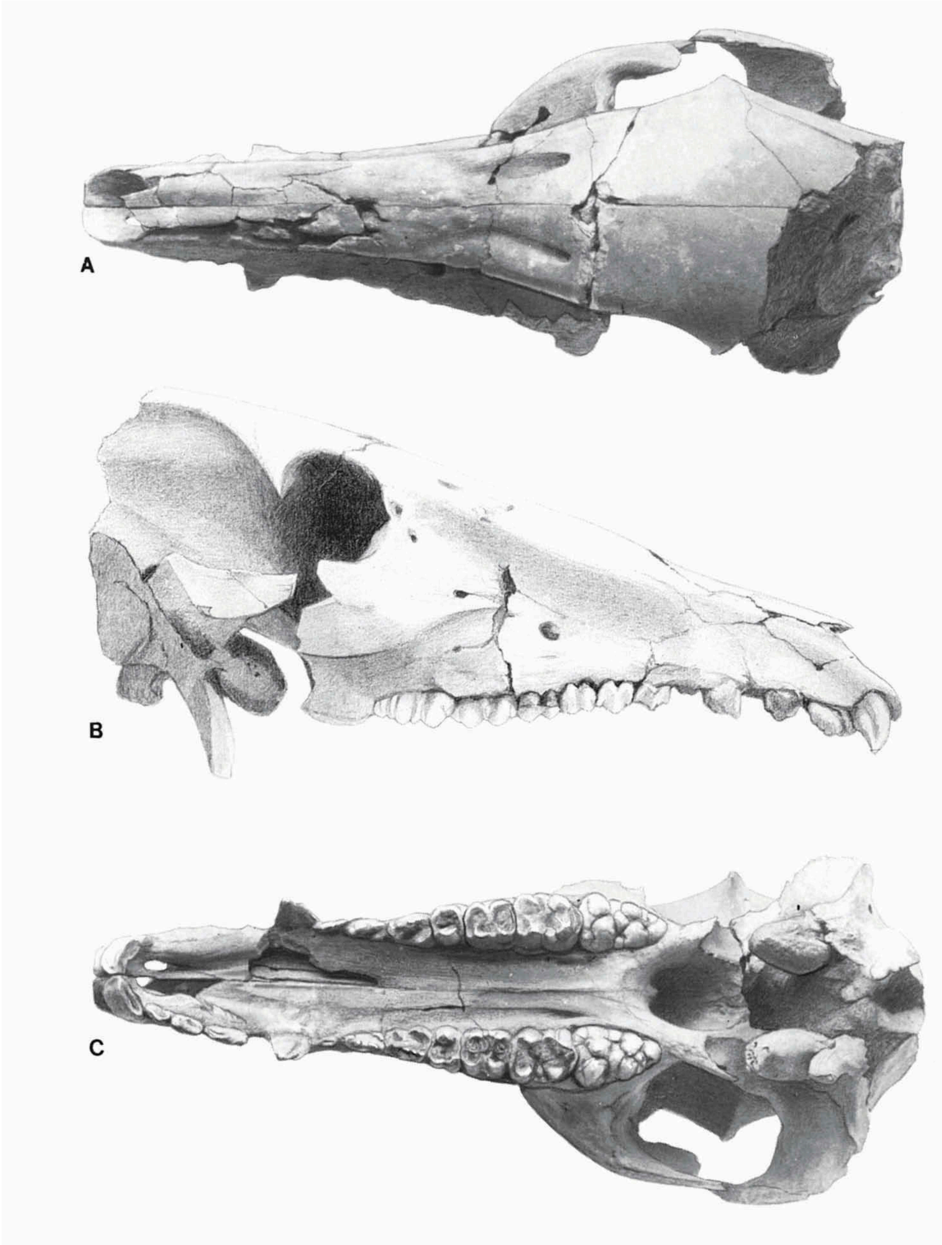
Description — The anterior part of the symphysis and the coronoid are missing. The dentition is almost complete, except for I_1 and I_2. The symphysial part resembles that of the lectotype, but the diastema between P_1 and P_2 is longer. The ramus is longer than the one in the lectotype. The lateral inflation is also lengthened. The posterior part of the ramus hardly differs from that of the lectotype, apart from the fact that it is longer.

Dentition — I_3 is almost the same as in *Sus verrucosus*. Its crown is 14.67 mm high. The canine is typically verrucosic. In this specimen it is larger than the lectotype.

Praemolars — The praemolars resemble those of the lectotype.

Molars — M_1 and M_2 are more or less the same as those of the lectotype; only M_1 is somewhat different. The M_3 is larger than the M_3 of the lectotype. Its talonid bears a larger median cusp. The morphology of the talonid, however, is still closer to the lectotype of *Sus brachygnathus* than to any other species. The inflation of the ramus is more elongated, as noted before.

Plate 3



Sus brachygnathus Dubois, 1908
Trinil s.s.
Fig. A. Skull of adult female, coll. Dub. 1862, dorsal view, approx. × 0.44.
Fig. B. Idem, lateral view, approx. × 0.44.
Fig. C. Idem, ventral view, approx. × 0.44.

Table 1. Measurements of seven mandible characters of *Sus brachygnathus* in the Dubois Collection, RMNH.

Cat. no.	1	2	3	4	5	6	7
1828	—	—	43.0	42.3	80.0	90.0	27.0
1845	—	—	44.0	34.0	81.6	100.0	34.0
1848	230.0	119.5	44.4	32.0	—	102.4	32.4
1861	247.0	—	48.5	32.0	69.5	99.8	32.7
185	261.0	135.0	48.6	33.0	69.5	109.1	37.5
n	3	2	5	5	4	5	5
min.	230.0	119.5	43.0	32.0	69.5	90.0	27.0
max.	261.0	135.0	48.6	42.3	81.6	109.1	37.5
$\bar{x}$	246.0	127.3	45.7	34.7	75.2	100.3	32.7
Log$\bar{x}$	2.39	2.10	1.66	1.54	1.88	2.00	1.51

1: Length of lower jaw; 2: height of lower jaw; 3: height of ramus; 4: thickness of ramus; 5: length of symphysis; 6: length of row of praemolars and molars; length of the third molar.

Syntype 3 — Left lower jaw, coll. Dub. 1848, Pl. 1, figs. A, E.

Locality — Trinil s.s.

Description — Left lower jaw with C-M_2, only M_2 and M_3 are complete. The root of the canine is open and clearly visible. The anterior part of the symphysis, in front of the canine, is missing. A prominent inflation on the left side ramus is probably caused by the protrusion of the canine root inside the ramus. The canine is worn posteriorly, about 35 mm from the top. The posterior width of the canine is 12.7 mm and the buccal width 15 mm. The diastema between P_1 and P_2 is 10 mm. For the teeth measurements see Table 2.

Dentition

Praemolars — P_1 is small, its top half is broken off. The morphology of P_1, however, is considered to be of little importance for suid taxonomy. P_2 has a single cusp; it is more or less triangular in shape, with the cusp in the middle. The sloping crown surface is faintly beaded and ribbed. P_3 resembles P_2, but the anterior surface is more abraded. The posterior stylid is well developed. P_4 is longer than P_3, and also large, but it is very much abraded. The postero-labial stylids are well developed.

Molars — M_1 and M_2 are similar to those of the lectotype. M_3 has three main pillars on the labial side. Three other minor pillars are present: one is situated antero-labially of the anterior main pillar, the second one on the labial side of the median valley, and the third one antero-buccally of the posterior main pillar. Two small accessory cusps are situated postero-buccally of the anterior main pillar, and antero-bucally of the middle main pillar. Due to its positon, the anterior minor pillar is part of the anterior cingulum. At the lingual side there are also three main lingual pillars: the anterior, the middle and the posterior one. The posteror one is part of the talonid. On this side we find two other minor pillars: the most anterior one is part of the cingulum. The other is situated antero-lingually of the posterior main pillar. There is yet another pillar situated behind the talonid main pillar row; it is also called the mid-terminal cusp. There are no accessory cusps in the median valley.

Syntype 4 — Right tibia, coll. Dub. 1903.

Locality — Trinil s.s.

Description — The proximal and distal parts of this specimen are in fair condition. The specimen shows a typical suid morphology, but it does not tell us very much about its taxonomic position. The tibia is smaller than that of *Sus verrucosus* (Recent species). As the teeth at Trinil are also smaller, this tibia might well belong to the same species as the teeth, viz. to *Sus brachygnathus*.

Measurements — Length: 181 mm; proximal width: 44.3 mm; distal width: 25.4 mm; smallest diameter of the shaft: 19.0 mm (near the distal end).

Syntype 5 — Left humerus, coll. Dub. 3261.

Locality — Trinil s.s.

Description — The proximal part of this specimen is in a poor condition. Near the proximal epiphysis we can still see the cartilage part which in this fossil (young individual) is filled with sand. The diaphysis (the shaft) is broken in the middle. The morphology of this humerus is suid-like. Its size is about the same as that of *Sus verrucosus*. As the teeth from Trinil are all of *Sus brachygnathus* this humerus can be accepted as being of the same species as the teeth.

Measurements — Length: 230 mm; proximal width: 70 mm; distal width: c. 50 mm; smallest width of the shaft: 27 mm.

Type specimen of Sus vatualangensis — A lower jaw, stored at the Geological Survey of Indonesia, Bandung.

Type-locality — Watualang, East Java.

Age — Pleistocene.

Remarks — *Sus vatualangensis* was described from the locality of Watualang, East Java. The diagnosis emphasises the difference in size between *Sus brachygnathus* and *Sus vatualangensis*. The only other differences between *Sus brachygnathus* and this species of von Koenigswald are that the M_3 of *Sus vatualangensis* is more elongated and the teeth have a more complicated morphology. All dental elements described of this species are slightly worn, and when these are compared with those of *Sus brachygnathus*, present in the same locality, the differences in complexity cannot be demonstrated. *Sus vatualangensis* should therefore be synonymised with *Sus brachygnathus*.

Sus macrognathus Dubois, 1908
Pl. 4.

Sus verrucosus, Dubois, 1891.
Sus macrognathus, Dubois, 1907, nomen nudum.
Sus macrognathus, Dubois, 1908.
Sus macrognathus, Stremme, 1911, part.
Sus macrognathus, von Koenigswald, 1933.
Sus coerti, von Koenigswald, 1934.
Sus verrucosus, Badoux, 1959.

Lectotype — M_3 sin., coll. Dub. 1713, Pl. 4, figs. A-B.

Type-locality — Kedungbrubus, East Java.

Diagnosis — Fossil pig larger than *Sus brachygnathus*, M_3 relatively longer. The median valley and talonid valley more clearly developed and less filled by the median cusp or median pillar. The talonid is more triangular than the talonid of *Sus brachygnathus*. The median posterior cusp has a terminal posterior position. The M^3 of this fossil pig is relatively longer than the one of *Sus brachygnathus*. In the median valley on the buccal side an accessory cusp is present which is larger and more complex than the same element of *Sus brachygnathus*. The talon has a more complex arrangement of its accessory cusp. The stylids on P^3 and P_4 are more pronounced than in *Sus brachygnathus*.

Remarks — A lectotype is chosen from the material of the Dubois collection. Stremme (1911) mentioned *Sus macrognathus* from Kedungbrubus as well as from Trinil. As Kedungbrubus produced a rich collection the lectotype is chosen from this locality. The specimen Stremme (1911) described also originates from Kedungbrubus.

Material — Kedungbrubus: M_3 sin., coll. Dub. 1713 (lectotype); M^3 dex., coll. Dub. 39-1; fragment of a right maxilla with P^4 and M^1, coll. Dub. 39-3; fragment of right mandibula with P_3 and P_4, coll. Dub. 39-2. Bangle: fragment of mandibula with M_3, coll. Dub. 7005-7.

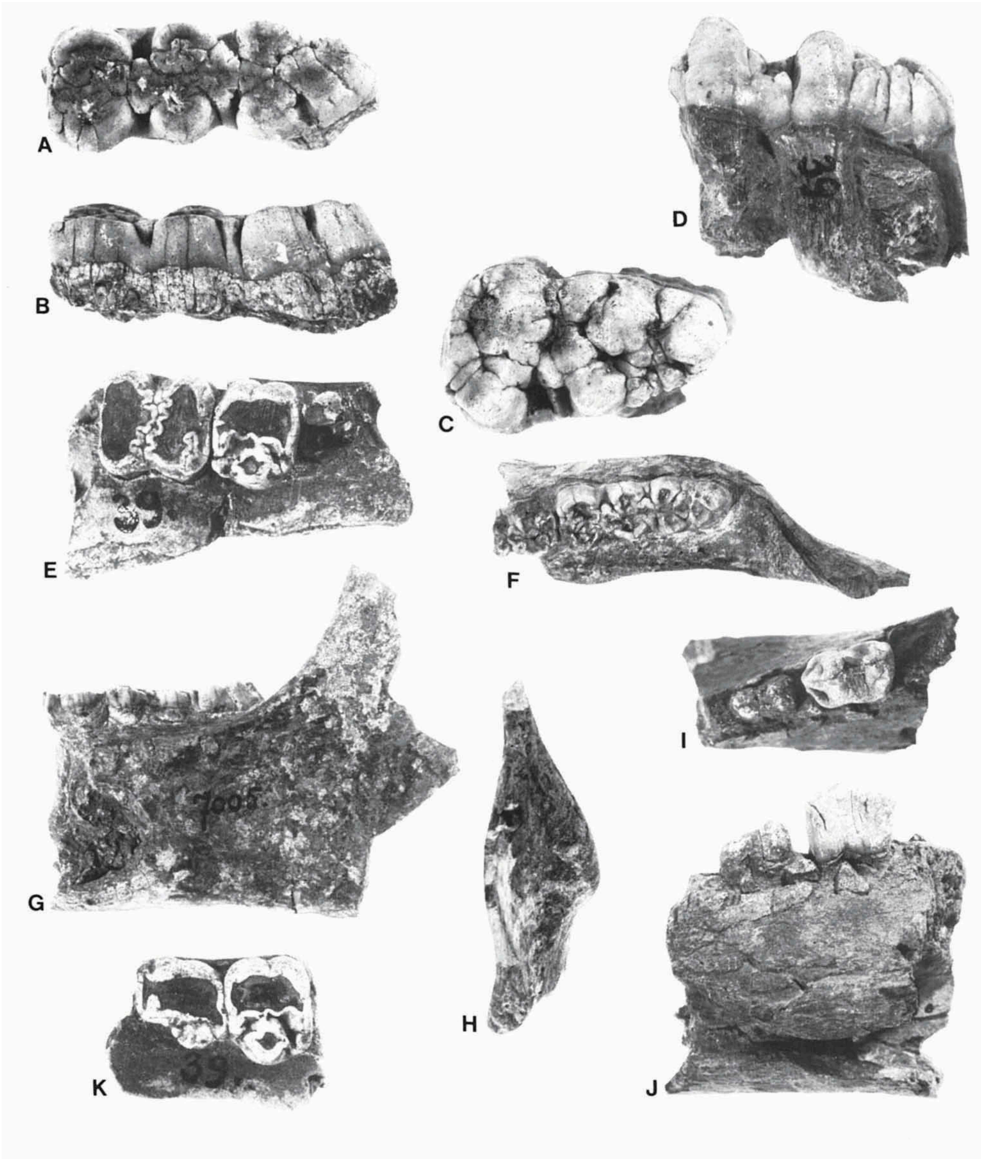
Description of the lectotype — The M_3 consists of 3 pairs of cusps and several median cusps. The cusps are worn, so they can also be called pillars. The pillars are distinct and separated from each other. The centre of the median valley is filled by the median pillar, and the centre of the talonid valley by a cusp called hypoconulid. There are no accessories at either end of the valley. The talonid of this specimen is almost triangular. The anterior part of the talonid is formed by the third row of cusps. Behind this pair there is a large median cusp which is divided into two almost separate smaller cusps. The accessory cusp is hardly visible; it is located at the posterior end of the lingual side of the third pair of cusps.

Measurements of the lectotype — The length of the tooth is 46.5, the width is 17.9 mm. The length of the talonid is almost half the length of the tooth. The anterior cingulum is more prominently developed on the buccal than on the lingual side (see Pl. 4, figs. A-B).

Syntype 1 — Fragment of a left lower jaw, coll. Dub. 7005-7, Pl. 4, figs. F-H.

Locality — Bangle, East Java.

Plate 4



Sus macrognathus Dubois, 1908
Fig. A. First lower molar (left), coll. Dub. 1713, occlusal view, approx. × 0.9.
Fig. B. Idem, buccal view, approx. × 0.9.
Fig. C. Third upper molar, coll. Dub. 39-1, occlusal view, approx. × 0.9.
Fig. D. Idem, buccal view, approx. × 0.9.
Fig. E. Fragment of upper jaw with P^4 and M^1, coll. Dub. 39-3, approx. × 1.0.
Fig. F. Fragment of left lower jaw with P^4 and M^1, coll. Dub.7005-7, top view, approx. × 0.45.
Fig. G. Idem, lateral view, approx. × 0.45.
Fig. H. Idem, rear view, approx. × 0.45.
Fig. I. Fragment of right ramus with P_4 and P_3, coll. Dub. 39-2, top view, approx. × 0.6.
Fig. J. Idem, lateral view, approx. × 0.6.
Fig. K. Fragment of right lower jaw with P_4 and P_3, top view, approx. × 1.0.

Description — This specimen consists of the posterior part of a ramus with M_3 and the posterior part of M_2. The M_3 is worn so much that only half of the cusps is left. The height of the ramus in front of the M_3 is c. 57 mm. The thickness of the ramus at the same point is 36.1 mm. The mental sinus can be seen because the anterior side of the specimen is open. The M_3 of this specimen has a longer and more slender shape than the same tooth of *Sus brachygnathus*. Its morphology is almost the same as that of the lectotype except that in its talonid valley, lingually, there is a small accessory cusp. The accessory cusp behind the third row is more clearly divided. The other accessory cusp, which is better developed, can be clearly seen lingually. The length of the talonid is about half that of the tooth. The length of M_3 is 47.0 mm, its width 17.7 mm. The tooth has three pairs of lateral cusps and three median cusps or pillars. One of the median pillars is located behind the first pair of pillars and structurally loose as if attached to the second pair of pillars. The second median pillar is in the talonid valley and is also called hypoconulid. The third pillar is situated medially behind the third pair of pillars, which seems to be transversally divided, so it consists of an anterior and a posterior part. At the posterior part of the tooth, the median terminal consists of two smaller cusps and in addition there are three small accessory cusps. The talonid is more complex than the talonid of the lectotype.

Syntype 2 — Fragment of an upper jaw, coll. Dub. 39-3, Pl. 4, fig. E.

Locality — Kedungbrubus, East Java.

Description — This specimen of *Sus macrognathus* is the right part of a maxilla with P^4 and M^1. The specimen is from a male individual. This can be concluded from the posterior part of the canine flange present above the posterior part of P^4. Part of the palatine is preserved and is 10 mm wide. Only the part of the maxilla with the roots of the teeth is present.

Teeth — The P^4 is almost square; there is a round cusp at the lingual side. Labially on the main cusp, an antero-posterior spill is present. Lingually, the tooth has an antero-posterior fold. The structure can be paralleled with the stylus of the third or fourth praemolar. Although the M^1 is longer, the width is more or less the same as that of the P^4. A small accessory cusp is present on the labial side. The tooth is divided by a very weak median valley. The edge of the anterior and posterior cusps consists of wavy enamel.

Syntype 3 — M^3, coll. Dub. 39-1, Pl. 4, figs. C-D.

Locality — Kedungbrubus, East Java.

Description — The tooth is well preserved and is only very slightly worn. The general shape is triangular. The anterior cingulum is developed. Two valleys are present: the median valley and the talon valley. The talon valley is less distinct than the median one. In the median valley labially there is a low folded structure, which also can be called the accessory cusp. Behind the second pair of cusps and in front of the median terminal cusp at the side, buccally there are five small accessory cusps which form the outer rim of the talon. Another single cusp is present at the lingual side. The tooth is 37.9 mm long and 23.8 mm wide.

Syntype 4 — Fragment of the ramus of a lower jaw with P^4 and P^3, coll. Dub. 39-2, Pl. 4, figs. I-J.

Locality — Kedungbrubus, East Java.

Description — P^4 is well preserved, whereas the P^3 is badly damaged. Since the ramus is open anteriorly, the root of the canine is visible. The canine is of the verrucosic type. The P^4 is unicuspid with accessory cusps on the anterior and posterior side. A stylus is present at the posterior part of the tooth on the buccal and on the lingual side. The stylus on the buccal side is more pronounced.

Remarks — According to von Koenigswald (1934, p. 191), *Sus coerti* differs from *Sus macrognathus* by having a very pronounced mandible inflation of the ramus. This species is based only on a mandible without teeth from the vicinity of Jetis, East Java. The exact locality is not known. Furthermore the specimen on which the new species is based is not figured. The writer considers this species not valid, and he synonymises it with *Sus m. macrognathus* Dubois.

Sus macrognathus terhaari von Koenigswald, 1933

Sus sp. Stehn & Umbgrove, 1929.
Sus terhaari von Koenigswald, 1933.
Sus verrucosus terhaari Badoux, 1959.

Type specimen — The type specimen is the hind part of a skull, selected from the collection of the Geological Survey in Bandung (M.G.K. 29), figured by von Koenigswald (1933, p. 155, pl. 14).

Type-locality — Ngandong, East Java.

Age — Late Pleistocene.

Diagnosis — Suid of verrucosic-type, larger than *Sus m. macrognathus*.

Description — See Diagnosis.

Measurements — Length of hind part of skull: 163.9 mm; width of occipital crest: 106.3 mm; width of jugal: 54.8 mm; occipital height: 150.5 mm; length of basioccipitoparasphenoid: 45.0 mm; bizygomatic width: 180.0 mm; length of M^3 dext. 41.8 mm; width of M^3 dext. 18.8 mm.

Paratype — Left mandible with P_1-M_3, M.G.K. 30, figured by von Koenigswald (1933, p. 157, pl. 15).

Locality — Watualang, near Ngawi, East Java.

Description — The left mandible is longer than that of *Sus macrognathus macrognathus*. The M_3 is very elongated when compared with that of *Sus brachygnathus* and *Sus m. macrognathus*.

Measurements — Length of lower jaw 281.4 mm (its tip is missing); height of ramus: 57.0 mm; height of lower jaw: 139.6 mm; thickness of lower jaw: 38.9 mm; length of P_2-M_3: 134.4 mm; length of M_1-M_3: 91.5 mm; length of M_3: 52.7 mm; width of M_3: 21.0 mm.

Other material examined — A hind part of a skull (M.G.K. 29), and fragments of a lower jaw with molars (M.G.K. 25, 31, 24).

Remarks — The identification of this material is based on the similarity in the length/width relation of the M_3 and the inflation of the ramus. These characters are not very specific and in this respect *Sus terhaari* is also close to *Sus verrucosus* and *Sus m. macrognathus*.

Sus terhaari overlaps in size with *Sus m. macrognathus*, however it is on average bigger. The validity of this species is questionable, and in my opinion the size difference points to a subspecific difference. According to von Koenigswald (1933), *Sus terhaari* is related to *Sus barbatus*.

Sus stremmi von Koenigswald, 1933

Sus stremmi, von Koenigswald, 1933.

Type — Von Koenigswald did not designate a type.

Age — Plio-Pleistocene (Kali Glagah fauna). Several levels of the Kaliglagah Formation were excavated by the Geological Survey. The fauna described so far originates from the formation as a whole and there are indications that different faunas have been mixed in the past (Sondaar, 1981; ter Haar, 1934). Ter Haar (1934) mentioned that a Jetis fauna might be present in the Kaliglagah Formation.

The specimens are insufficiently documented so it cannot be concluded whether they originated from the top or from the basis of the Kaliglagah Formation. The only indication which might give some idea about the level is the fact that von Koenigswald (1933) mentioned that the specimens came from 'laag XIV'. In the collection at the Geological Survey in Bandung, there are specimens of *Mastodon* with the indication: 'ingraving B, laag IX/X' (excavation B, bed IX/X). *Mastodon* probably occurs at the base of the Kaliglagah Formation. If the layers have been numbered systematically this implies that the material of *Sus stremmi* came from a higher level. Since the old locality data are rather vague one cannot make a clear statement about the stratigraphical position of *Sus stremmi*.

Remarks — *Sus stremmi* is based only on very limited material from Bumiayu: three praemolars, a third upper molar and two canines (von Koenigswald, 1933, p. 49). The M^3 has the shape of an M_3 and is rather elongated, while the posterior part is broad and not triangular. In size it resembles *Sus macrognathus* most, but due to the aberrant morphology (length-width ratio does not match with either an M^3 or an M_3) we do not want to place this fossil in that species.

The morphology of *Sus stremmi* (M.G. Coll. K. 44)resembles that of *Sus macrognathus*. Due to the small number of specimens and the unkown stratigraphical position, *Sus stremmi* must be considered a nomen dubium.

Sus sangiranensis von Koenigswald, 1963

Sus sangiranensis von Koenigswald, 1963.

Type — Type specimen is an M^3 stored in the Senckenberg Museum, Frankfurt.

Type-locality — Sangiran, Central Java.

Age — Middle Pleistocene.

Description — The smallest pig in Java found so far, smaller than the extant pig in Indonesia, *Sus celebensis*. The M^3 is primitive (von Koenigswald, 1963); its outline is triangular, and its talon simple. No accessory cusps are present; the secondary cusps (conulets) block the valleys. The anterior valley is restricted to the central part.

The measurements for M^3 from Sangiran are: length 16.3 mm and width 10.8 mm.

Remarks — The diagnosis of *Sus sangiranensis* by von Koenigswald (1963) is based only on one M^3 and one P^4 selected from the vast material from different levels. According to the author this species has primitive and simple teeth. I had an opportunity to see the type material in Frankfurt. The M^3 is indeed very small and the talon is not fully developed. Since the species is based on only two dental elements, the exact locality and stratigraphic level of which are not documented, it is difficult to decide whether we are dealing with aberrant specimens or a really distinct species. The species needs to be re-evaluated.

DISTRIBUTION OF THE SPECIES

General remarks

Suid fossils are quite common in the various localities of Java. The fossils studied can be classified in several morphotypes, which corroborate the various species described in the next chapter. If they differ essentially from the species described so far they will be described separately. The material studied consists mainly of isolated teeth, which were measured and analysed biometrically (Hardjasasmita, 1982).

The localities (Fig. 11)

Bangle — The material consists of 3 M_2, 4 M^2, 20 M_3, and 9 M^3. In the material from Bangle two different forms of *Sus* can be distinguished, mainly on the basis of their size differences (see Figs. 12-13). The size of the small form and the morphology of its teeth resemble those of *Sus brachygnathus* from Trinil s.s. although there is a slight size difference, the specimens from Bangle being somewhat larger. The large form resembles *Sus macrognathus* in size and morphology.

The major part of the material falls within the variation of *Sus macrognathus*. If we take the M_3 as an example (N = 20), 80% can be attributed to this species.

Kaligede — The morphology of the dental elements from this locality does not differ from that of *Sus brachygnathus*. The size of the specimens falls within the variation of this species. There is some confusion about the locality of Kaligede (de Vos, pers. comm.);

there are probably two levels, one of which can be compared with that of Trinil (see Table 2).

Table 2. Measurements of the third molars of *Sus brachygnathus* and of *Sus macrognathus* from Trinil s.s., Sumberkepuh, Kebonduren, Kedungbrubus, and Kaligede.

Coll. Dub.	element	*Sus brachygnathus* length	width	*Sus macrognathus* length	width
Trinil s.s.					
1848	M_3	30.0	14.6		
1847	M_3	30.7	14.1		
1827	M_3	31.0	15.1		
1688	M_3	31.0	16.6		
6203	M_3	31.6	14.5		
1837	M_3	31.6	14.6		
1861	M_3	32.2	16.2		
1837	M_3	32.7	15.4		
1855	M_3	32.9	16.3		
1845	M_3	34.2	15.7		
1854	M_3	37.8	17.0		
Sumberkepuh, East Java					
716	M_3			44.1	19.2
716	M_3			38.0	19.5
Kebonduren, East Java					
1833	M_3	33.0	15.3		
83 7	M^3	31.0	20.0		
1836	M_3			42.0	17.5
83 a	M_3			43.3	17.5
83 b	M_3			47.5	17.5
Kedungbrubus					
1713	M_3			46.5	17.9
39	M^3			37.9	23.9
41	M^3			42.1	21.3
Kaligede					
1713	M_3	29.1	14.5		
1875 1	M_3	33.0	14.5		
1875 3	M_3	33.8	15.9		
1875 4	M_3	34.4	17.7		
1875 5	M_3	34.9	16.9		
1875 6	M_3	35.6	16.9		
1875 7	M_3	35.9	17.2		
1875 8	M_3	36.5	18.8		
1875 9	M_3	38.6	19.1		
1875 10	M_2	16.5	11.8		
1875 11	M_2	19.0	13.4		
1875 12	M_2	19.5	13.5		
1875 13	M_2	19.5	13.5		
1875 14	M^3	28.5	19.8		
1875 15	M^3	28.6	20.0		
1875 16	M^3	30.0	17.5		
1875 17	M^3	30.6	19.4		
1875 18	M^3	30.9	18.9		

Teguan — In this locality two morphotypes are present, which resemble *Sus brachygnathus* and *Sus macrognathus*. There is not much material (see Table 3) available but *Sus macrognathus* is more abundant than *Sus brachygnathus*. In this respect the pig fauna from this locality resembles that from Bangle (see Table 3).

Table 3. Measurements of molars of *Sus brachygnathus* and *Sus macrognathus* from Bangle and Teguan.

Coll. Dub.	element	*Sus brachygnathus*		*Sus macrognathus*	
		length	width	length	width
Bangle					
714 1	M_3	31.5	15.0		
716	M_3	33.7	16.5		
875 101	M_3	34.1	15.7		
715 1	M_3	35.5	17.0		
715 2	M_2	20.0	13.5		
714 2	M_2	20.0	14.8		
715 3	M^3	29.0	19.0		
714 3	M^3	29.2	17.1		
714 4	M^3	29.9	18.2		
714 5	M^3	30.3	19.3		
714 6	M^3	32.0	19.1		
715 4	M^3	33.0	20.0		
38	M^2	20.0	13.5		
714 41	M_3			42.3	16.7
716 8	M_3			43.0	17.9
714 31	M_3			44.5	16.4
38 5	M_3			45.4	17.0
7005 1	M_3			45.5	19.5
38 7	M_3			45.5	16.8
38 6	M_3			46.0	17.2
7005 2	M_3			47.0	18.0
7005 7	M_3			47.8	17.6
1289 2	M_2			23.7	15.5
538 1	M^3			43.3	23.8
538 2	M^3			43.6	21.1
715	M^3			42.4	21.3
38 8	M^2			21.3	20.4
1829 3	M^2			25.0	19.0
1829 1	M^2			25.4	23.0
Teguan					
1859	M_3	32.7	16.7		
1835	M_3	33.5	16.0		
1859	M_2	19.0	15.0		
1835	M_3			44.4	19.0
1838	M_3			45.0	18.1
1844	M^3			37.1	23.3
1826	M^3			39.2	19.1
1826	M^3			39.2	21.2
1835	M^3			39.3	24.5
1835	M^2			22.7	17.0
1844	M^2			24.0	18.5
1835	M^2			28.1	20.2

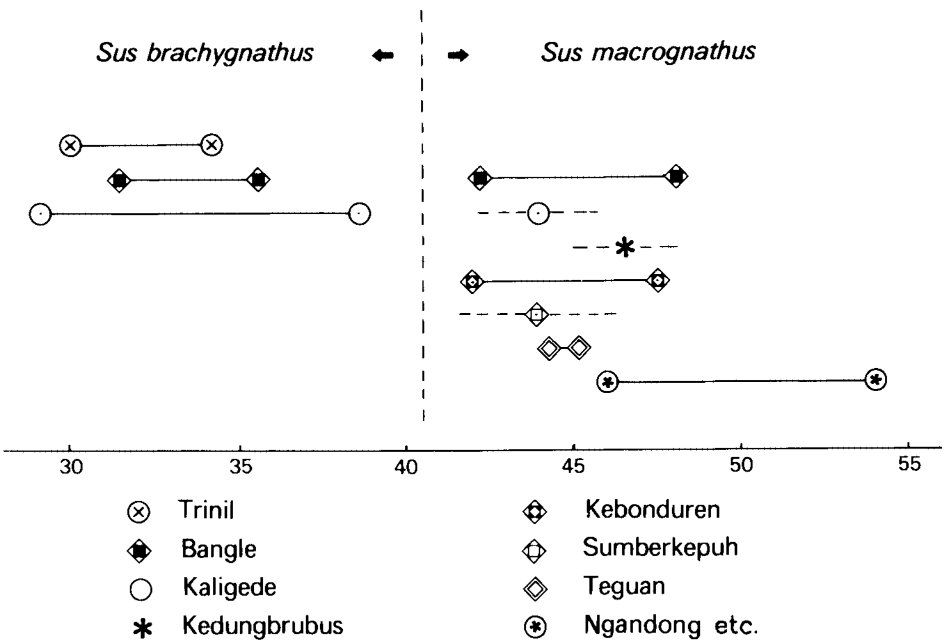


Fig. 12. Diagram showing maximum and minimum length of M_3 of *Sus brachygnathus* and *Sus macrognathus* from various localities on Java.

Kebonduren — In this locality *Sus brachygnathus* and *Sus macrognathus* are present. Unfortunately there are only a few specimens in the collection: 4 M^3, 3 M_2, 1 M^2, and 1 M^3. The majority of the specimens belong to *Sus macrognathus*. In this respect the pig fauna resembles that from Bangle.

Sumberkepuh — Very few data from this locality are available. There is only one tooth (M_3) present in the collection of Dubois in Leiden. It matches the M_3 of *Sus macrognathus* morphologically, and the size is within the range of that species.

Sangiran

General remarks — The studied collection of pigs from Sangiran, Central Java, originates from a large area around the village of Sangiran and no precise locality data are available. The fossils and the geology of the Sangiran area have been studied by von Koenigswald (1933, 1940), the Indonesia-Japan Research Group (Anonymous, 1979) and by Sartono et al. (1980, 1981a). It is clear that in this area several (3) fossiliferous levels are exposed, containing fossils of different ages. The material from Sangiran was collected by the villagers; therefore no data are available about the level from which they came. The material studied is stored in Bandung (Dept. Geology, ITB; Geological Survey of Indonesia) and in the Senckenberg Museum, Frankfurt. According to von Koenigswald (pers. comm.) the specimens in his collection in the Senckenberg Museum were bought and no stratigraphical data are available.

Discussion — It was not possible to separate the fossils into different morphotypes; as had been possible in the case of the material from Kebonduren and Bangle. There is a large variation in size, larger than the variation in *Sus brachygnathus* and *Sus macrognathus* (see Figs. 14-17; Tables 4-5).

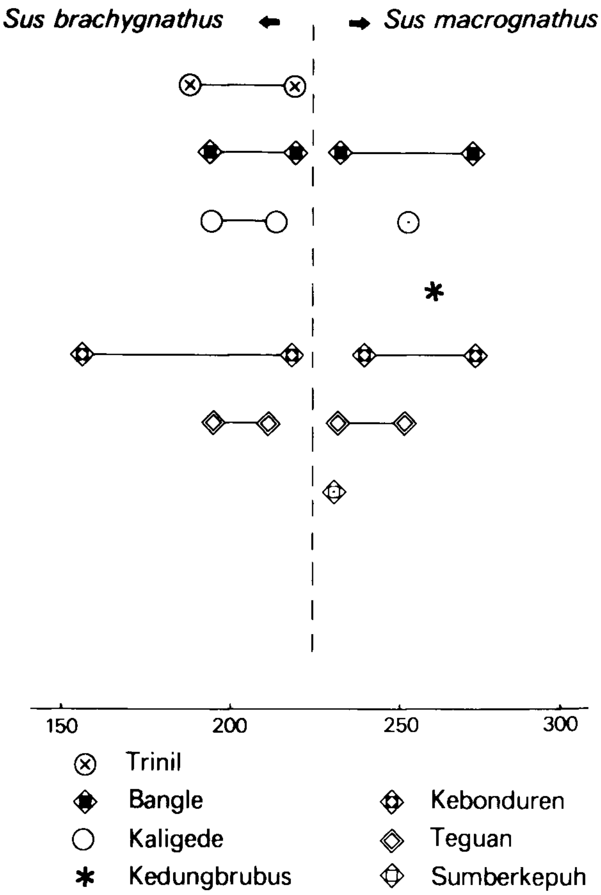


Fig. 13. Diagram showing the range of the length-width ratio of M_3 of *Sus brachygnathus* and *Sus macrognathus* from various localities on Java.

Table 4. Maximum and minumum length/width ratio of M_3 of *Sus brachygnathus* and *Sus macrognathus* from several localities on Java.

locality	maximum	minimum	species
Trinil	218	187	*Sus brachygnathus*
Bangle	217	204	*Sus brachygnathus*
	217	233	*Sus macrognathus*
Kaligede	212	194	*Sus brachygnathus*
	—	252	*Sus macrognathus*
Kedungbrubus	—	260	*Sus macrognathus*
Kebonduren	216	155	*Sus macrognathus*
	271	240	*Sus brachygnathus*
Teguan	209	196	*Sus macrognathus*
	249	233	*Sus macrognathus*
Sumberkepuh	—	230	*Sus macrognathus*

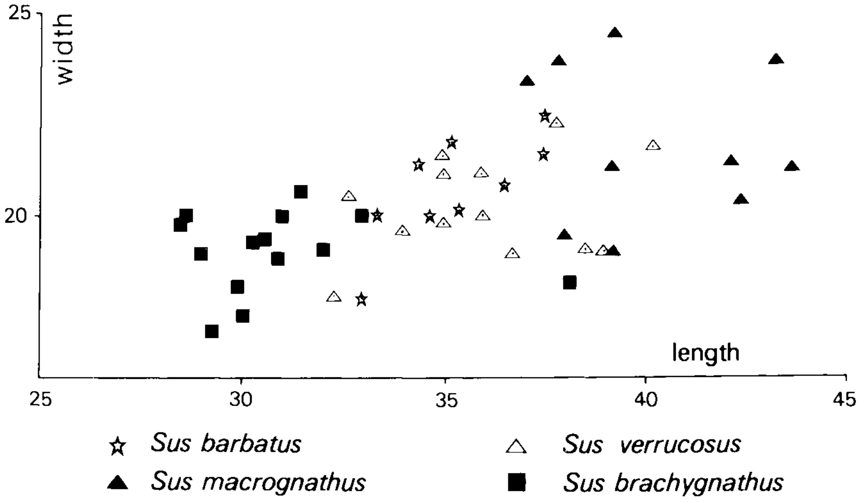


Fig. 14. Length-width diagram of M^3 of two fossil species (*Sus macrognathus* and *Sus brachygnathus*) and two extant species (*Sus barbatus* and *Sus verrucosus*).

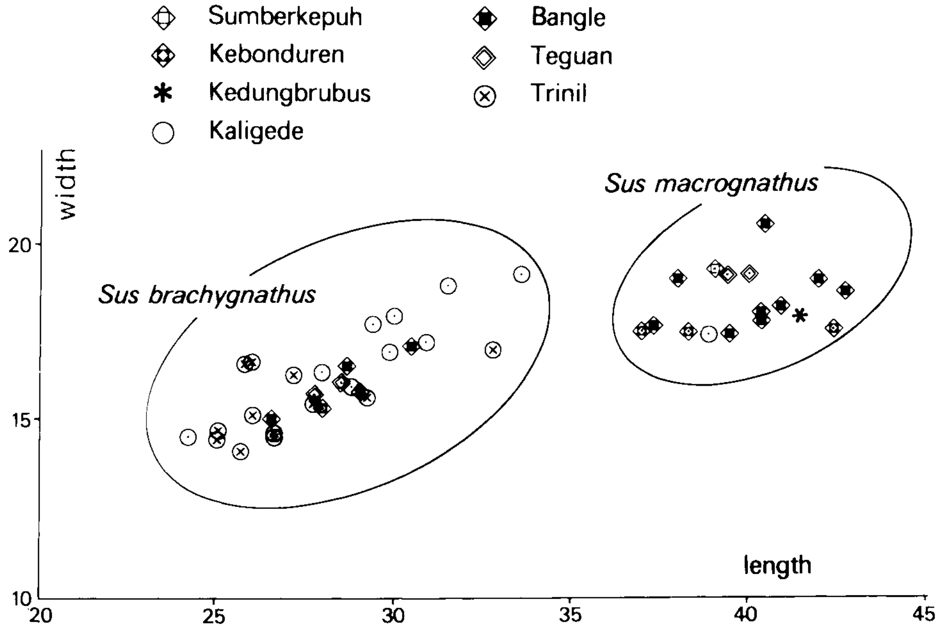


Fig. 15. Length-width diagram of M_3 of two fossil species (*Sus brachygnathus* and *Sus macrognathus*) from different localities on Java.

Table 5. Range in size of fossil teeth of *Sus* from Sangiran, central Java.

	length n	min.	max.	mean	width min.	max.	mean
M_3	105	25.0	42.1	32.1	11.0	21.3	15.2
M^3	146	23.4	40.0		14.8	24.0	

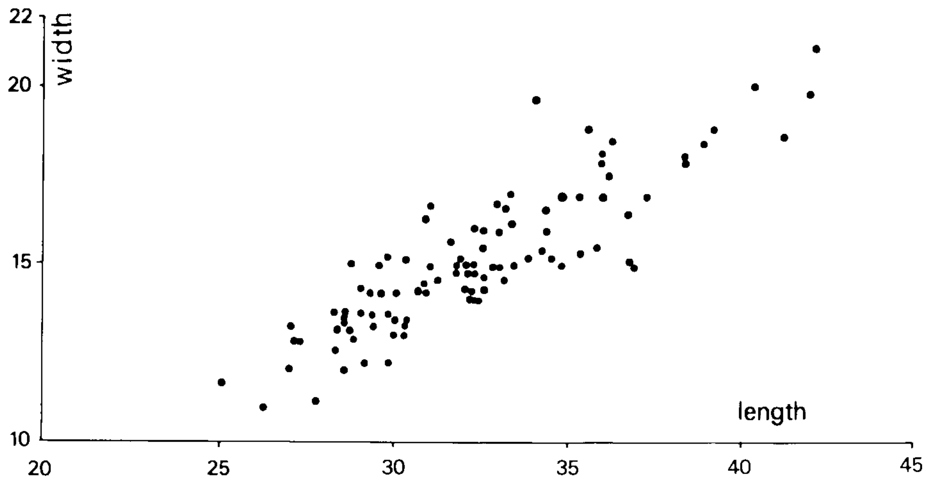


Fig. 16. Length-width diagram of M_3 of fossil *Sus* from Sangiran, Central Java.

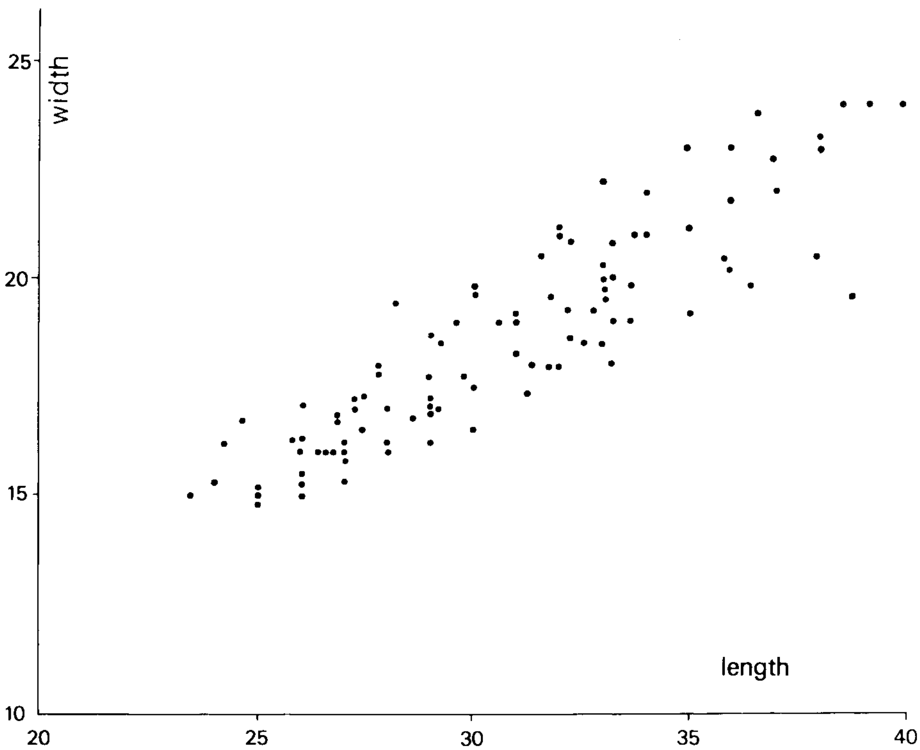


Fig. 17. Length-width diagram of M^3 of fossil *Sus* from Sangiran, Central Java.

From the material studied it can be said that the morphotypes of *Sus brachygnathus* and *Sus macrognathus* are present. Due to the fact that material from different levels is mixed and the general morphology of different pig species bears a close resemblance, it is impossible to separate the different species on the basis of teeth morphology alone. One skull from Sangiran, in the collection of the Institute for Earth Science, Utrecht, clearly is of the same size and has the same morphotogy as that of *Sus brachygnathus*. The diagnostic characters of the skull are: naso-frontal straight; orbits larger than in *Sus celebensis* (vertical diameter: 40.3 mm; horizontal diameter: 36.4 mm); palatine narrow (M^2-M^3 is 25.3 mm); no crista, as in *Sus barbatus*; supra-orbital process clearly visible, jugal width exceeds that of *Sus celebensis*. The skull is not well preserved. It is compressed in such a way that the palatine and the left orbit are facing the same surface. The dentition (P^4-M^3) is well preserved. The measurements of the teeth are given in Table 6.

Table 6. Measurements of molars and praemolars of fossil *Sus* from Sangiran, Central Java.

	P^4	M^1	M^2	M^3
Length	10.8	16.0	21.3	30.8
Width	13.0	15.2	18.6	20.0

The length of M^1-M^3 is 67 mm. The stylus on the P^4 dext, situated antero-labially, is clearly visible. The size variation of the material from Sangiran is extremely large (see Figs. 16-17). *Sus brachygnathus* and *Sus macrognathus* from Sangiran overlap in the scatter diagram and cannot be separated. The overlapping is considered to be due to the fact that material from different stratigraphical levels is mixed. The variation is larger than that observed in the material from localities such as Bangle, Kaligede, Teguan, etc.; in those localities there are clearly two groupings. Such groupings cannot be demonstrated in the scatter diagram of the material from Sangiran.

If we compare the various scatter diagrams we can draw the following conclusions. In Figs. 14-15 the length and width of the upper and lower third molar from Bangle are represented; two different groups can be distinguished. The smaller form is comparable with *Sus brachygnathus* from Trinil, while the larger form resembles *Sus macrognathus*. The teeth of *Sus macrognathus* are more elongated than those of *Sus brachygnathus*; this was also noted by von Koenigswald (1933), who observed a relative lengthening of the M^3, compared to M^1 and M^2 in *Sus macrognathus* (see von Koenigswald, 1933, fig. 3).

If we put all the data from the various localities excavated by Dubois into one scatter diagram, the diagram resembles the one from Sangiran. In other words this corroborates the statement that the material from Sangiran is mixed and originates from different levels. In the collections from Trinil s.s. only one species is present. One larger M_3 is considered to be an aberrant specimen. The size of the M_3 of *Sus macrognathus* is more or less the same in all localities. In *Sus brachygnathus* there is some difference in size. The fossils from Teguan are practically the same as those from Trinil. From Kebonduren only on M_3 is available. The specimens from Bangle are larger than those from Trinil. The Kaligede specimens are also larger than those from Trinil although one specimen is smaller. The diagrams show that the size of the M_3 of *Sus macrognathus* from Kedungbrubus, Bangle, Kebonduren, and Kaligede is more uniform than that of *Sus brachygnathus* from the same localities.

FOSSIL FORMS COMPARED WITH EXTANT SPECIES

Since the fossil material consists mainly of isolated teeth and only a little skull material, we have to base the taxonomy mainly on the morphology and size of the dental elements. The diagnostic characters for distinguishing *Sus scrofa* and *Sus verrucosus* are the shape

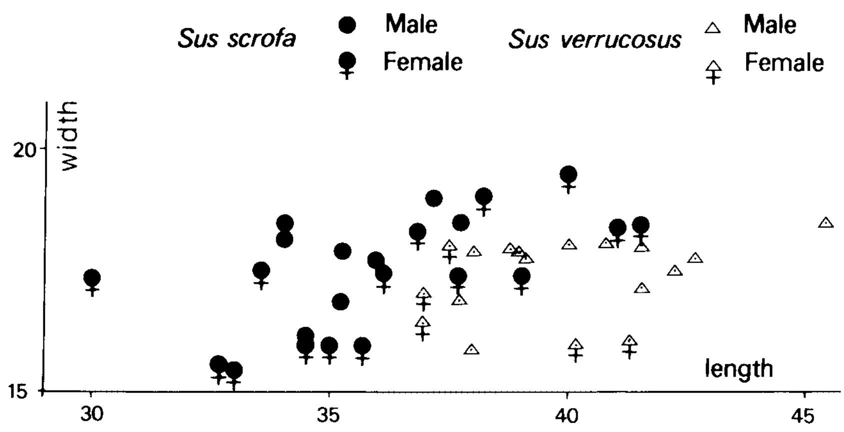


Fig. 18. Length-width diagram of M_3 of male and female *Sus scrofa* and *Sus verrucosus*.

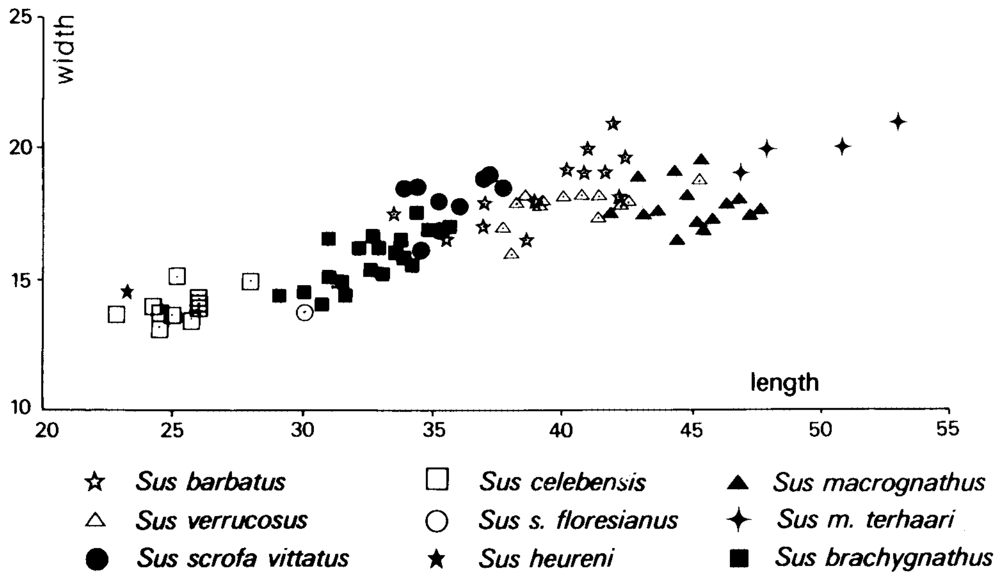


Fig. 19. Length-width diagram of M_3 of the genus *Sus*: fossil and extant species.

of the lower male canine and the morphology of the M^2 and M^3. In *Sus verrucosus* these teeth show a better developed stylus (Pl. 5). The size of the M_3 of *Sus verrucosus* is intermediate between the M_3 of *Sus brachygnathus* and that of *Sus macrognathus* (see Figs. 18-19).

Morphology of the skull

By comparing some of the measurements of the skull of various species we observe that the palatine in *Sus brachygnathus* is shorter than it is in *Sus celebensis, Sus verrucosus* and *Sus barbatus*. The skull is also narrower; and so is the jugal. On the basis of the material in the RMNH, the skull of *Sus brachygnathus* seems to be smaller.

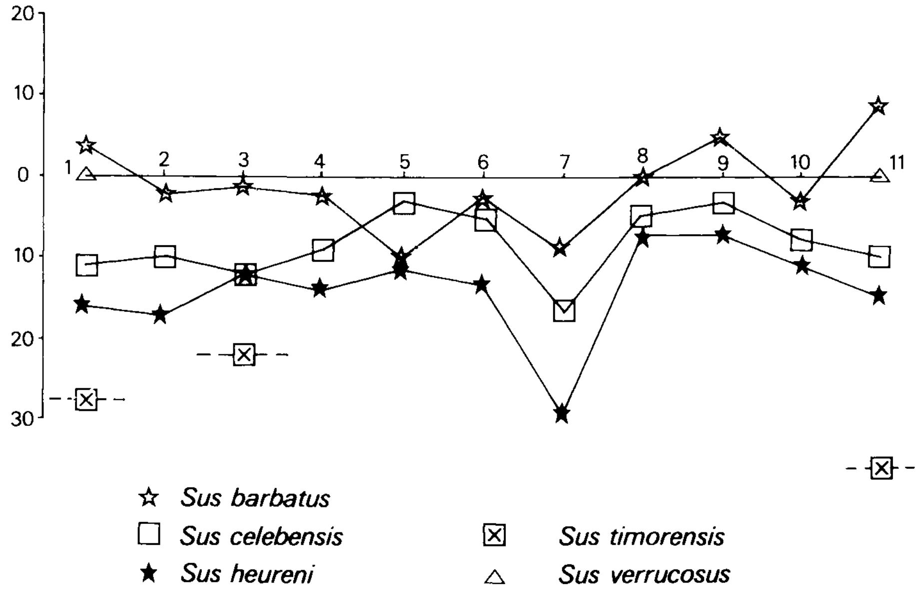


Fig. 20. Diagram showing the differences (× 100) of the logarithms of the mean of the measurements of the skull of *Sus barbatus, Sus celebensis, Sus heureni, Sus timorensis,* and *Sus verrucosus* compared with *Sus verrucosus*.
1 – length of skull: tip of maxilla to back of occipital crest; 2 – length of rear skull: supraorbital foramen to back of occipital crest; 3 – bizygomatic; 4 – bizygomatic at the point of anterior socket of the eyes; 5 – occipital width: width across occipital crest; 6 – occipital height: posterior rim of foramen magnum to top of occipital crest; 7 – width of zygomatic jugal: jugal height; 8 – width of eye socket; 9 –height of eye socket; 10 – length of basioccipitosphenoid: tip of basisphenoid to hypoglossal foramina; 11 – palate length.

Orbit — The orbits of *Sus brachygnathus* are relatively smaller than the orbits of *Sus barbatus* and *Sus verrucosus*; however, they are of the same size as the orbits of *Sus celebensis*. The diagram (Fig. 20) shows that the horizontal diameter of the orbit in *Sus brachygnathus* is smaller than in the three extant species. Even so, in general view, the orbit of *Sus brachygnathus* seems to be larger.

Lower jaw — The morphology of the lower jaw of *Sus brachygnathus* is rather similar to that of *Sus celebensis*, although it is longer. *Sus celebensis* has a 216.5 (203.0-230.6) mm long and *Sus brachygnathus* a 254.0 mm long lower jaw. Compared to the jaw of *Sus verrucosus* the mandibula of *Sus brachygnathus* is shorter and more inflated.

Morphology of the teeth — The morphology of the teeth, other than the third molar, is about the same as that of the corresponding elements of *Sus celebensis* and *Sus verrucosus*. The M_3 of *Sus brachygnathus* is longer and wider than the M_3 of *Sus celebensis* but shorter than the M_3 of *Sus verrucosus*. The talonid of the M_3 of *Sus brachyugnathus* is more complex than the talonid of *Sus celebensis*, but less complex than that of *Sus verrucosus*. One of the characters common to *Sus verrucosus* and *Sus celebensis* is that the stylus of the P^3 and the stylid of the P_3 and P_4 are all more pronounced than those of the same teeth of *Sus scrofa*. The cross-section of the male lower canine also resembles that of the extant species, *Sus verrucosus* etc. They have the verrucosic type of male lower canine.

RECENT SUIDS OF INDONESIA

Introduction

The various extant species of *Sus* have been established mainly on their external morphology. So far the teeth morphology and various skull characters have not been fully described. Previous authors did not provide measurements of dental elements; these are essential for comparing the extant species with the fossil ones. In the present paper those characters will be studied in a special way, so that the extant forms can be compared with the fossil forms. The characters of the teeth and some skull characters will be added to the already known external characteristics of the Recent forms. The genus *Babyrousa* has been revised by Groves (1980), and will not be discussed in this study.

Descriptions

Sus verrucosus Müller & Schlegel, 1845
Pl. 5.

Sus verrucosus Müller & Schlegel, 1845.
Sus verrucosus, Jentink, 1905.
Sus verrucosus, Lydekker, 1915.
Sus verrucosus, Chasen, 1940.
Sus verrucosus verrucosus, Laurie & Hill, 1954.

Type — A male skull, cat. Ost. d, RMNH.

Type-locality — Java, exact locality unknown.

Revised diagnosis — Wild pig with moderately sized skull. The skull is larger than that of *Sus scrofa vittatus, S. s. milleri* and *Sus celebensis* but smaller than that of *Sus barbatus*. The profile of the skull is a straight line. The brain is rather flat at the fronto-parietal part. The parietal constriction is wide. The snout is longer than in *Sus celebensis* and in *S.s. vittatus*, but it is shorter than in *Sus barbatus*. The maxilla flange is only slightly developed but has a low lateral flange crest, which is more developed than in *S.s. vittatus*. The zygomatic arch is wide and more inflated anteriorly. The facial crest is strong. The orbits are relatively small. The male lower canine is of the verrucosic type; its size is moderate, but smaller than the same element in *Sus barbatus*. The mandible is inflated. The occipital is wide and the median ridge is poorly developed. The external auditory canal opening is placed higher above the foramen magnum. The praemolars, especially the third and fourth, have a more pronounced stylus and stylid than in *Sus scrofa vittatus* and *Sus scrofa milleri*.

Description — Lateral profile almost a straight line, slight change of slope at naso-frontal suture. Orbit located below fronto-parietal surface. Frontal and parietal areas are gently arched. The width of parietal constriction is narrow but much wider than the width of the snout. Brain case below parietal crest more or less vertical. Occipital wider than that of the other species, and a marked median ridge, although not very prominent, is present. Nasal parallel-sided, or narrowed in the middle, gently rounded, curving into near-vertical side walls of the maxilla. The upper border of the praemaxilla is situated almost above the P_2. The posterior end of the infra-orbital foramen is located above the P^4. The canine flange is moderately developed, and the lateral crest is low. The base of the zygomatic arch makes an angle of c. 45° with the axis of the skull; posteriorly it sweeps smoothly to the lateral wall, which is nearly vertical. The zygomatic process of the malar bone is thicker and broader and also more inflated than that of the other species. The lower border of the zygoma is curved. The origin of the levator rostri is high-up, and is deeply scooped. The ridge below the levator rostri is relatively strong and sharp anteriorly. The origin of the depressor rostri is moderately developed and deeply scooped. The stylus and stylid are present on the buccal side of the upper and lower praemolars. The upper canine is flattened and has an oval cross-section. A strong medial ventral groove and a weak medial dorsal groove are present. The lower canine is moderately developed with the outer surface markedly wider than the posterior surface, and only slightly narrower than the inner surface. The last lower molar is long and shows three pairs of lateral pillars. A terminal median cusp forms the posterior part of the talonid. Various other cusps are present on the talonid. Accessory cusps occasionally occur on the talonid.

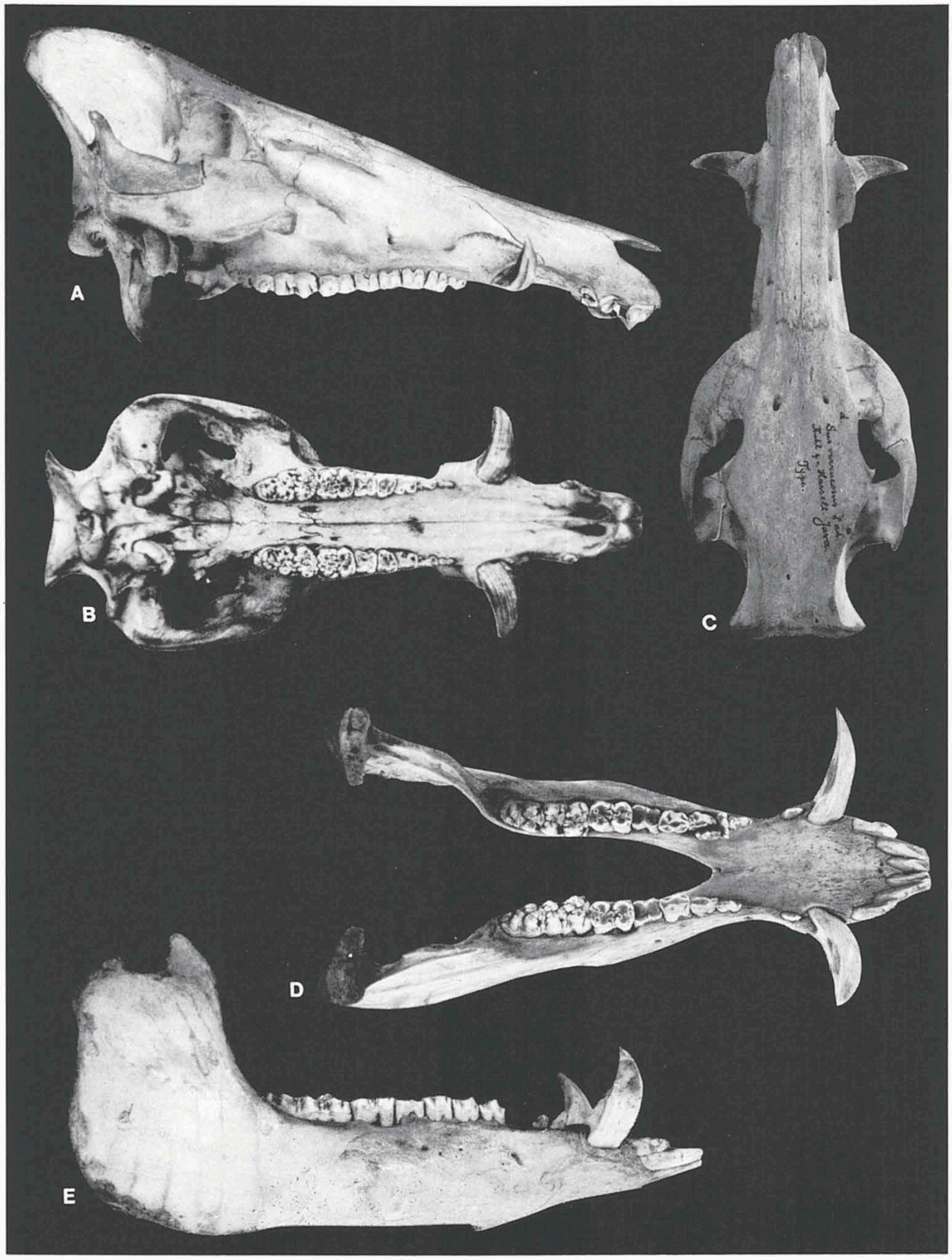
Measurements — The measurements of the skull and jaw of *Sus verrucosus* are presented in Tables 7-8 and Figs. 19-22. From the figures it can be deduced that the length of the lower jaw, of the symphysis and of P_2-M_3 are smaller than in *Sus scrofa vittatus*. The thickness of the corpus of the lower jaw is larger and the M_3 is longer in *Sus verrucosus* than in *Sus barbatus* and in *Sus s. vittatus*. *Sus verrucosus* has the longest and also the largest M_3. The length of the palatine of *Sus verrucosus* is 246.62 mm and its total skull length is 404.45 mm.

Table 7. Measurements of eleven skull characters of *Sus verrucosus*, coll. RMNH.

Cat. no.	1	2	3	4	5	6	7	8	9	10	11
2659	370.3	145.3	154.3	139.0	82.9	120.6	42.3	37.9	34.2	35.3	230.0
Sody S58	377.2	143.3	155.7	143.7	85.7	125.7	46.0	39.0	25.0	31.0	235.5
Sody 1	385.0	145.0	150.0	139.0	84.0	129.0	43.2	42.0	36.0	34.0	230.0
2657	402.0	152.7	153.0	153.0	96.3	145.0	48.5	39.0	35.0	34.0	241.0
Ost.d	403.1	142.8	164.2	164.2	91.8	132.0	46.9	37.2	35.1	31.1	258.0
Ost.1	406.5	160.0	160.0	145.0	83.6	137.0	43.5	42.0	36.0	34.8	243.0
Ost.1	407.0	151.0	156.2	150.0	84.8	138.5	41.0	38.8	35.4	35.4	241.6
1175	415.3	157.2	171.6	156.0	82.6	140.0	46.3	41.9	35.4	36.8	246.0
2655	415.7	164.0	175.0	150.6	91.3	147.0	52.0	41.4	37.2	33.3	242.6
Sody 23	420.0	152.7	153.0	153.0	96.3	145.0	48.5	39.0	35.0	34.0	241.0
1172	420.6	165.2	162.7	148.0	87.5	137.0	51.3	42.6	39.2	32.2	252.8
1231	430.7	171.2	168.8	147.0	89.2	143.5	50.5	42.7	37.9	32.9	257.3
n	12	12	12	12	12	12	12	12	12	12	12
min.	370.3	142.8	150.0	139.0	82.6	120.6	41.0	37.2	25.0	31.0	230.0
max.	430.7	171.2	175.0	164.2	96.3	147.0	52.0	42.7	39.2	36.8	258.0
$\bar{x}$	404.5	154.2	160.4	149.0	88.0	136.7	46.7	40.3	35.1	33.7	243.2
Log$\bar{x}$	2.61	2.19	2.21	2.17	1.94	2.14	1.67	1.61	1.55	1.53	2.39

1: Length of skull: tip of maxilla to back of occipital crest; 2: length of the hind part of skull: supra-orbital foramen to back of occipital crest; 3: bizygomatic width; 4: bizygomatic width at the point of anterior socket of the eyes; 5: occipital width: width across occipital crest; 6: occipital height: posterior rim of foramen magnum to top of occipital crest; 7: width of zygomatic jugal: jugal height; 8: width of eye socket: horizontal; 9: height of eye socket; 10: length of basioccipitosphenoid: tip of basisphenoid to hypoglossal foramina; 11: length of palatine.

Plate 5



Sus verrucosus Müller & Schlegel, 1845
Java, exact locality unknown, Recent.
Fig. A. Skull of adult male, holotype, cat. Ost. d, lateral view, approx. × 0.22.
Fig. B. Idem, ventral view, approx. × 0.22.
Fig. C. Idem, dorsal view, approx. × 0.22.
Fig. D. Mandible of adult male, holotype, cat. Ost. d, top view, approx. × 0.22.
Fig. E. Idem, lateral view, approx. × 0.22.

Table 8. Measurements of seven mandible characters of a male *Sus verrucosus*, coll. RMNH (for an explanation of the character numbers see Table 1).

Cat. no	1	2	3	4	5	6	7
2670	300.0	124.0	58.8	31.0	94.4	119.6	42.3
e	298.1	125.0	57.0	37.3	97.3	112.7	38.8
1231	297.2	120.2	49.7	35.6	97.0	116.4	42.7
1172	295.2	132.6	53.2	35.0	94.0	103.0	41.5
1175	292.2	115.6	50.6	35.6	88.0	117.6	39.1
d	291.0	135.9	57.3	33.0	86.6	120.2	45.4
2657	289.0	118.5	55.3	31.5	86.0	124.3	41.5
1233 e	288.6	111.3	51.3	30.0	87.0	116.2	37.6
2655	288.0	115.0	50.7	30.7	85.3	117.8	40.0
1	284.5	123.8	48.9	33.0	81.0	115.0	37.7
Sody 58	273.0	126.7	48.5	31.5	81.5	114.0	38.0
2659	265.7	118.8	46.7	31.3	79.0	118.0	39.2
1224	260.0	121.0	45.0	32.0	82.0	116.7	40.8
n	13	13	13	13	13	13	13
min.	260.0	111.3	45.0	30.0	79.0	103.0	37.6
max.	300.0	135.9	58.8	37.3	97.3	124.3	45.4
$\bar{x}$	286.3	122.2	51.8	32.9	87.6	116.3	40.4
log$\bar{x}$	2.46	2.09	1.71	1.52	1.94	2.07	1.61

Sus barbatus Müller, 1838
Pl. 6.

Sus barbatus Müller, 1838.
Sus barbatus, Jentink, 1905.
Sus barbatus, Miller, 1906.
Sus barbatus, Lydekker, 1915.
Sus barbatus, Chasen, 1940.
Sus barbatus, Medway, 1967.
Sus oi, Jentink, 1905, part.

Type — An adult female skeleton, cat. Jentink 1887, a, RMNH.

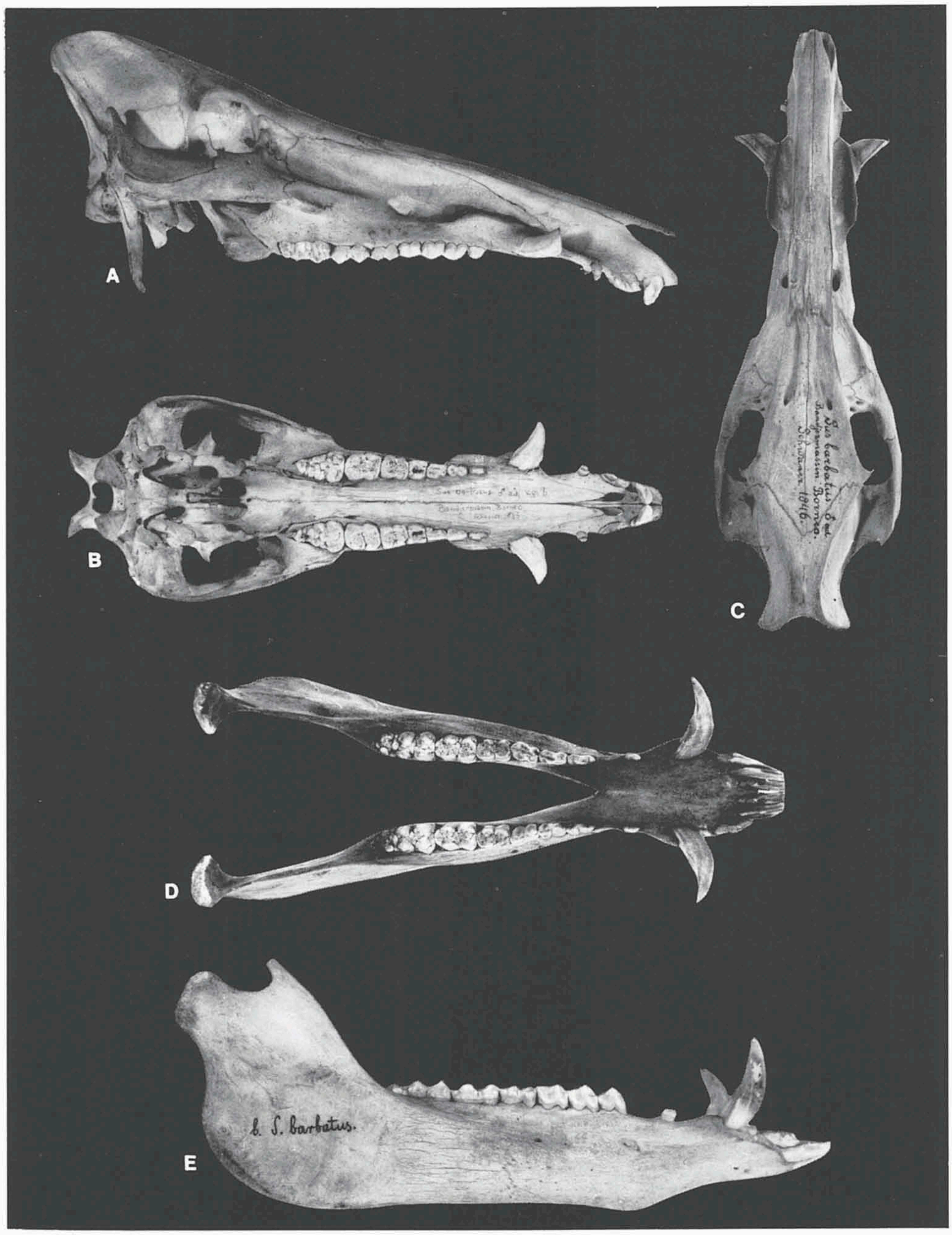
Type-locality — The village of Pululampey, near Banjarmasin, southeast Kalimantan (Borneo).

Revised diagnosis — Large extant pig from Indonesia. Skull long, low and narrow (see Tables 9-10; Figs. 19-21). Head same as skull, long, low and narrow with bare muzzle, with long, curved tuft of bristles on cheeks; ears small; tail with a large terminal tuft; young striped (Jentink, 1905). Canine of verrucosic type, nasal slender, M_3 shorter than M_3 of *Sus verrucosus*. The length of the skull, snout, palatine, and the lower jaw is the largest of all extant species of pig of Indonesia. The head profile is concave starting from the naso-frontal suture. The auditory bullae are the thinnest of all suids in Indonesia. The parietal crest is more pronounced than in the other species of pig in Indonesia.

Description

The skull — The skull (RMNH cat. b) is very elongated and narrow across the zygomatic arch. The malar and the maxilla bones slope down from behind the infra-orbi-

Plate 6



Sus barbatus Müller, 1838
Pululampey, near Banjarmasin, southeast Kalimantan (Borneo); Recent.
Fig. A. Skull of adult male, RMNH cat. b, lateral view, approx. × 0.19.
Fig. B. Idem, ventral view, approx. × 0.19.
Fig. C. Idem, dorsal view, approx. × 0.19.
Fig. D. Mandible of adult male, RMNH cat. b, top view, approx. × 0.19.
Fig. E. Idem, lateral view, approx. × 0.19.

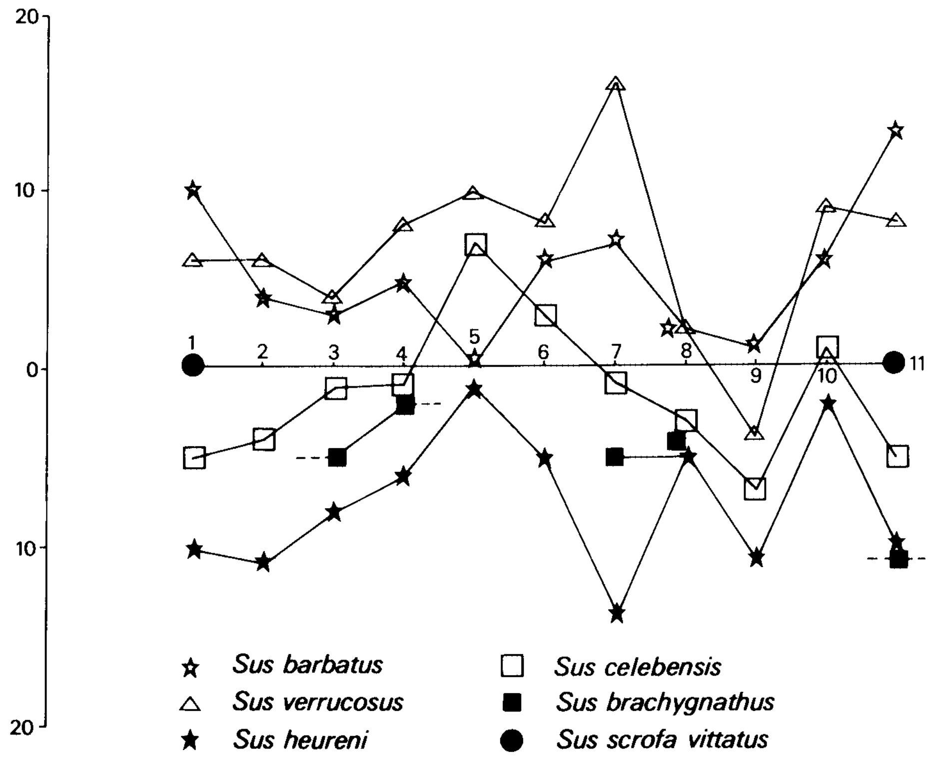


Fig. 21. Diagram showing the differences (× 100) of the logarithms of the mean of the measurements of the skull of *Sus barbatus, Sus verrucosus, Sus heureni, Sus celebensis, Sus brachygnathus,* and *Sus scrofa vittatus* compared with *Sus scrofa vittatus*. Same legend as for Fig. 20.

tal foramen. The upper part of the skull is slightly concave. The crista sagitalis starts at the parietal. It is 12 mm wide. The bony palate extends far beyond the last molars (c. 45 mm). The praemaxilla extends a few millimetres beyond the incisors. This last character is also found in *Sus celebensis*.

Sus celebensis Müller & Schlegel, 1845
Pls 7-8.

Sus celebensis Müller & Schlegel, 1845.
Sus celebensis, Jentink, 1905.
Sus celebensis, Lydekker, 1915.
Sus celebensis, Hooijer, 1950.
Sus celebensis, Hooijer, 1969.
Sus verrucosus celebensis, Laurie & Hill, 1954.
Sus nehringii, Jentink, 1905, part.
Sus weberi, Jentink, 1905.

Types — A male skull, cat. Ost. b, RMNH; a female skull, cat. Ost. c, RMNH.

Type-locality — Mando, North Sulawesi (Celebes).

Table 9. Measurements of eleven skull characters of *Sus barbatus*, coll. RMNH (for an explanation of the character numbers see Table 7).

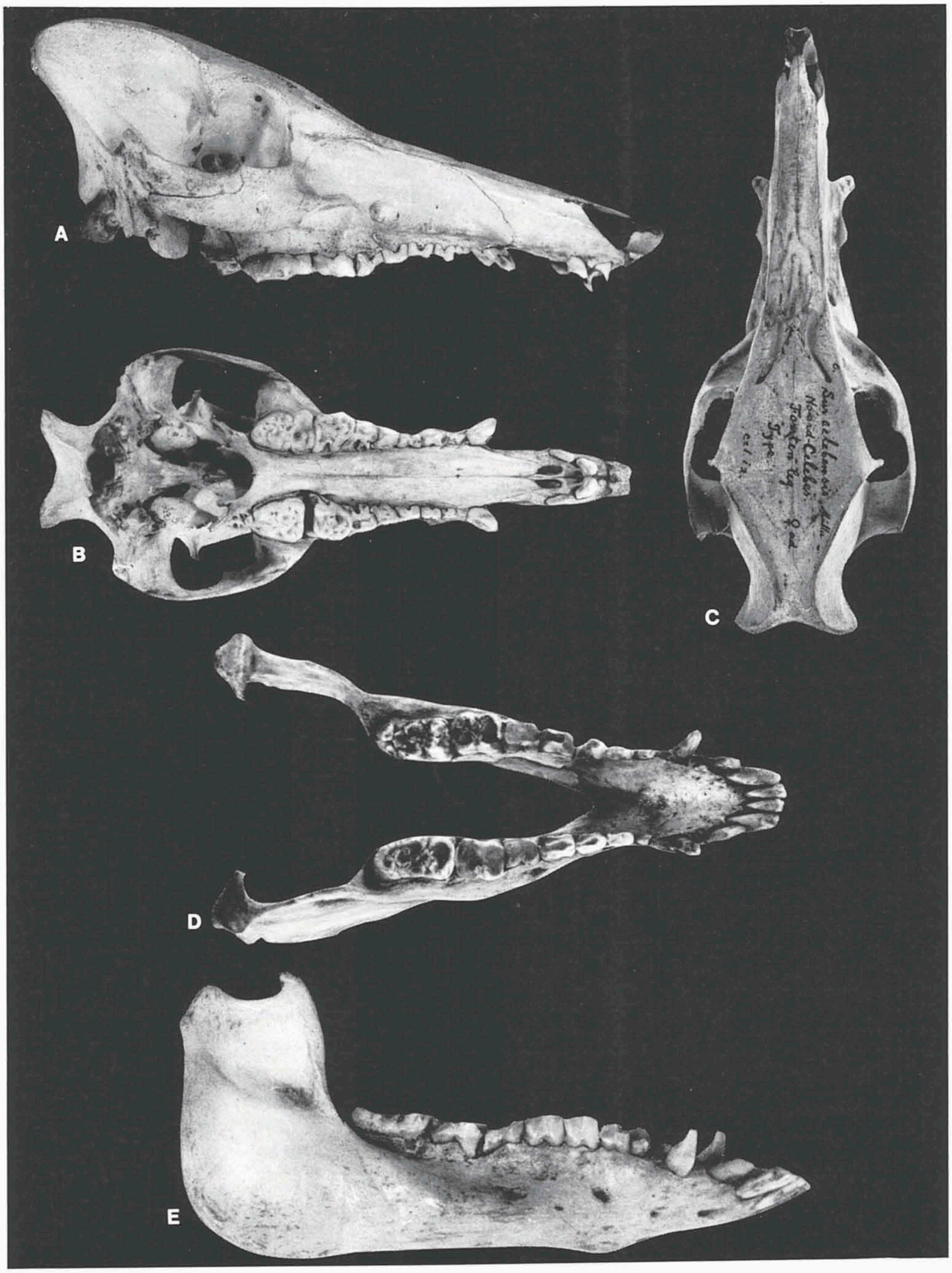
Cat. no.	1	2	3	4	5	6	7	8	9	10	11
1846c	412.5	136.3	137.0	123.5	63.2	119.0	29.4	39.1	41.0	27.7	280.3
Sody 28	420.0	146.5	147.5	133.0	63.0	122.0	33.7	40.3	37.5	30.0	294.3
1894	443.2	147.0	156.4	137.0	64.8	126.2	35.4	39.4	40.2	35.6	315.0
1846 b	443.2	147.0	156.4	138.5	64.8	126.2	35.4	40.2	43.5	30.0	306.7
11376	449.0	150.1	156.0	139.3	72.2	123.6	41.2	39.2	39.0	26.4	265.0
1887	517.0	151.0	170.0	—	72.8	135.2	42.8	38.2	39.4	39.5	313.0
Sody G 32	457.0	144.6	151.7	143.0	79.5	136.0	47.7	40.5	30.1	29.4	318.0
Diard c	480.0	161.3	174.0	153.3	77.0	139.0	39.6	40.7	40.3	34.3	326.5
n	8	8	8	7	8	8	8	8	8	8	8
min.	412.5	136.3	137.0	123.5	63.0	119.0	29.4	38.2	30.1	26.4	265.0
max.	517.0	161.3	174.0	153.3	79.5	139.0	47.7	40.7	43.5	39.5	326.5
x̄	452.7	148.0	156.1	138.2	69.7	128.4	38.2	39.7	38.9	31.6	302.4
logx̄	2.66	2.17	2.19	2.14	1.84	2.11	1.58	1.60	1.59	1.50	2.48

Table 10. Measurements of seven mandible characters of *Sus barbatus*, coll. RMNH (for an explanation of the character numbers see Table 1).

Cat. no	1	2	3	4	5	6	7
1846 b	293.0	123.7	47.1	25.0	88.5	116.4	33.5
Sody 28	304.0	129.2	48.5	—	93.4	115.5	35.5
Sody 1937	320.5	128.0	60.0	32.0	122.0	120.1	39.0
1137 b	322.0	140.7	51.7	29.2	116.3	130.7	42.5
Sody G.32	329.5	142.7	51.6	29.0	105.3	121.7	38.6
1846 c	332.0	130.5	54.4	32.0	114.0	125.3	41.8
1887	336.0	125.0	52.2	31.7	102.4	128.5	42.3
1894	336.0	130.8	50.1	25.6	113.7	125.4	40.2
Diard c	338.1	116.5	52.3	33.2	123.8	118.6	41.0
n	9	9	9	8	9	9	9
min.	293.0	116.5	47.1	25.0	88.5	115.5	33.5
max.	338.1	142.7	60.0	33.2	123.8	128.5	42.5
x̄	323.5	129.7	52.0	29.7	108.8	122.5	39.4
logx̄	2.51	2.11	1.71	1.47	2.04	2.09	1.60

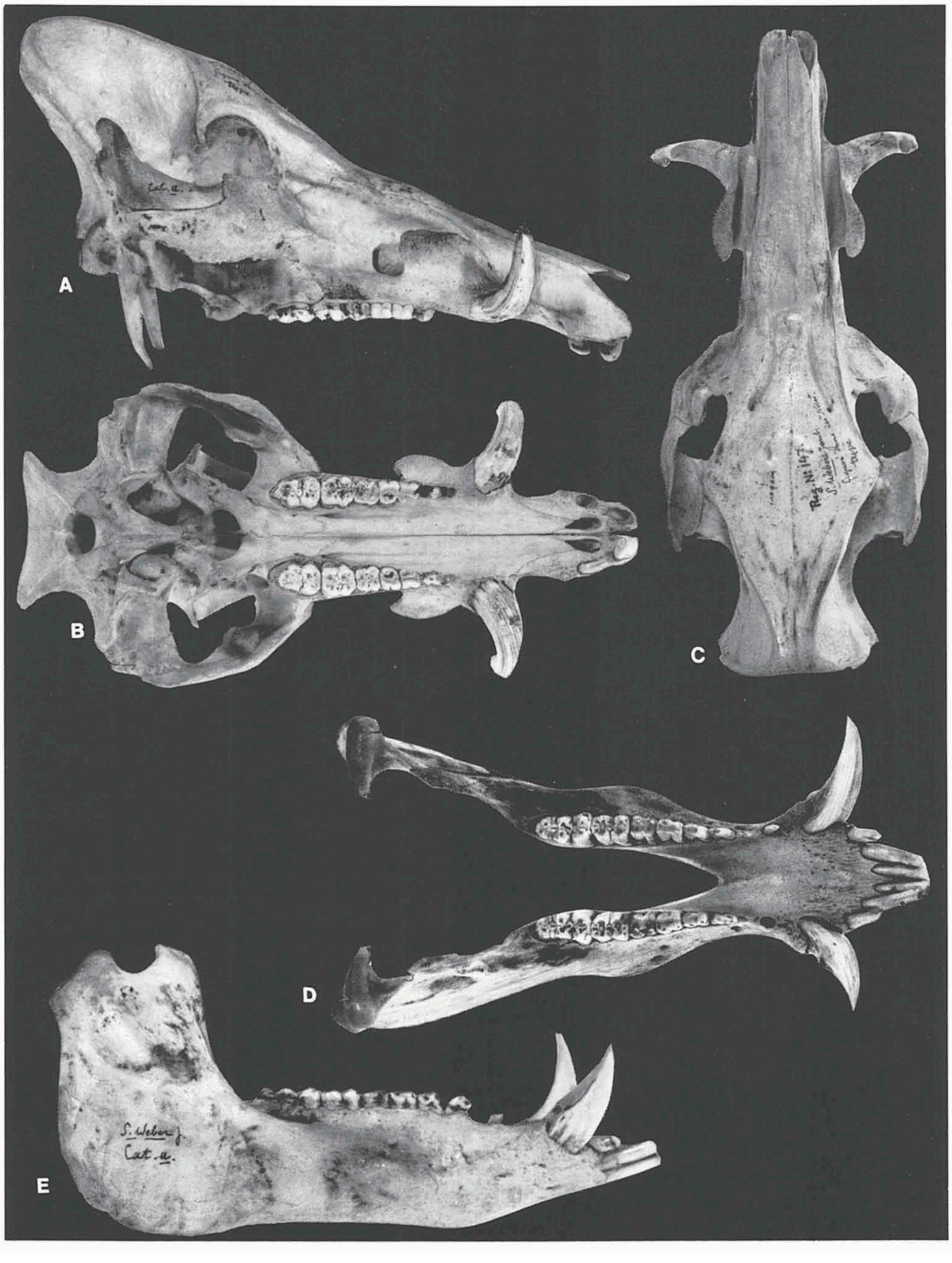
Revised diagnosis — The smallest pig of Sulawesi; smaller than *Sus scrofa vittatus, S. s. milleri* and *Sus verrucosus* (see Tables 11-12; Figs. 19-21). The male lower canine, P^3, P_3, and P_4 resemble those of *Sus verrucosus*. The skull profile is concave starting at the naso-frontal suture, in which respect it resembles the skull of *Sus barbatus*, although the skull of *Sus celebensis* is far shorter and smaller. The general appearance of the skull of *Sus celebensis* is stouter and not so elegant. The skull is short and high. The skin colouration is somewhere in between that of *Sus scrofa* and *Sus verrucosus* (Jentink, 1905). The young have stripes as do those of *Sus scrofa vittatus*. Facial markings are as in *S. s. vittatus*. A distinct, light-coloured tuft is present at the rear part of the cheek. The molars are shorter than in the two species mentioned before. The last upper molars of the type specimen are 24 mm (left), 25 mm (right), and the last lower molars are 25 mm (left) and 27 mm (right).

Plate 7



Sus celebensis Müller & Schlegel, 1845
Mando, North Sulawesi (Celebes); Recent.
Fig. A. Skull of adult female, cat. Ost. c, lateral view, approx. × 0.26.
Fig. B. Idem, ventral view, approx. × 0.26.
Fig. C. Idem, dorsal view, approx. × 0.26.
Fig. D. Mandible of adult female, cat. Ost. c, top view, approx. × 0.26.
Fig. E. Idem, lateral view, approx. × 0.26.

Plate 8



Sus celebensis Müller & Schlegel, 1845
Type of the conditionally proposed species *Sus weberi* Jentink, 1905.
Salyer Island, Recent.
Fig. A. Skull of adult male, ZMA B147, lateral view, approx. × 0.26.
Fig. B. Idem, ventral view, approx. × 0.26.
Fig. C. Idem, dorsal view, approx. × 0.26.
Fig. D. Mandible of adult male, ZMA 147, top view, approx. × 0.26.
Fig. E. Idem, lateral view, approx. × 0.26.

Table 11. Measurements of eleven skull characters of *Sus celebensis*, coll. RMNH and ZMA (for an explanation of the character numbers see Table 7).

Cat. no.	1	2	3	4	5	6	7	8	9	10	11
1192	302.0	114.7	137.0	111.0	72.3	109.4	28.5	—	—	29.0	187.5
1191	304.0	117.3	136.0	120.1	80.0	114.5	33.0	30.2	33.9	27.5	180.0
a	312.0	117.5	137.0	111.0	86.5	116.0	27.8	—	—	26.0	175.0
ZMA 1155	334.0	128.5	146.6	130.0	85.4	120.0	33.0	38.8	33.0	31.8	196.0
ZMA 147	338.0	139.6	152.0	136.2	86.0	129.0	36.0	37.2	33.6	27.2	196.3
N	5	5	5	5	5	5	5	3	3	5	5
min.	302.0	114.7	136.0	111.0	72.3	109.4	27.8	30.2	33.0	26.0	175.0
max.	338.0	139.6	152.0	131.2	86.5	129.0	36.0	38.8	33.9	31.8	196.3
x̄	318.0	123.5	141.7	121.7	82.0	117.8	31.7	35.4	33.5	28.3	187.0
logx̄	2.50	2.09	2.15	2.09	1.91	2.07	1.50	1.55	1.53	1.45	2.27

Table 12. Measurements of seven mandible characters of *Sus celebensis*, coll. RMNH and ZMA (for an explanation of the character numbers see Table 1).

Cat.no.	1	2	3	4	5	6	7
1192	203.0	100.3	41.6	26.8	59.6	94.0	25.0
1191	209.0	99.2	40.3	25.8	62.0	91.5	26.5
a	219.0	100.0	44.5	26.6	80.0	84.0	24.5
1155 ZMA	221.0	95.6	41.2	25.8	76.3	88.1	27.5
147 ZMA	230.6	114.2	41.1	29.5	74.1	87.0	25.2
n	5	5	5	5	5	5	5
min.	203.0	95.6	40.3	25.8	59.6	84.0	24.5
max.	230.6	114.2	44.5	29.5	80.0	91.5	27.5
x̄	216.5	101.9	41.7	26.9	70.4	88.9	25.7
logx̄	2.34	2.01	1.62	1.43	1.85	1.95	1.41

Sus heureni sp. nov.
Pl. 9.

Sus celebensis, Groves, 1981.

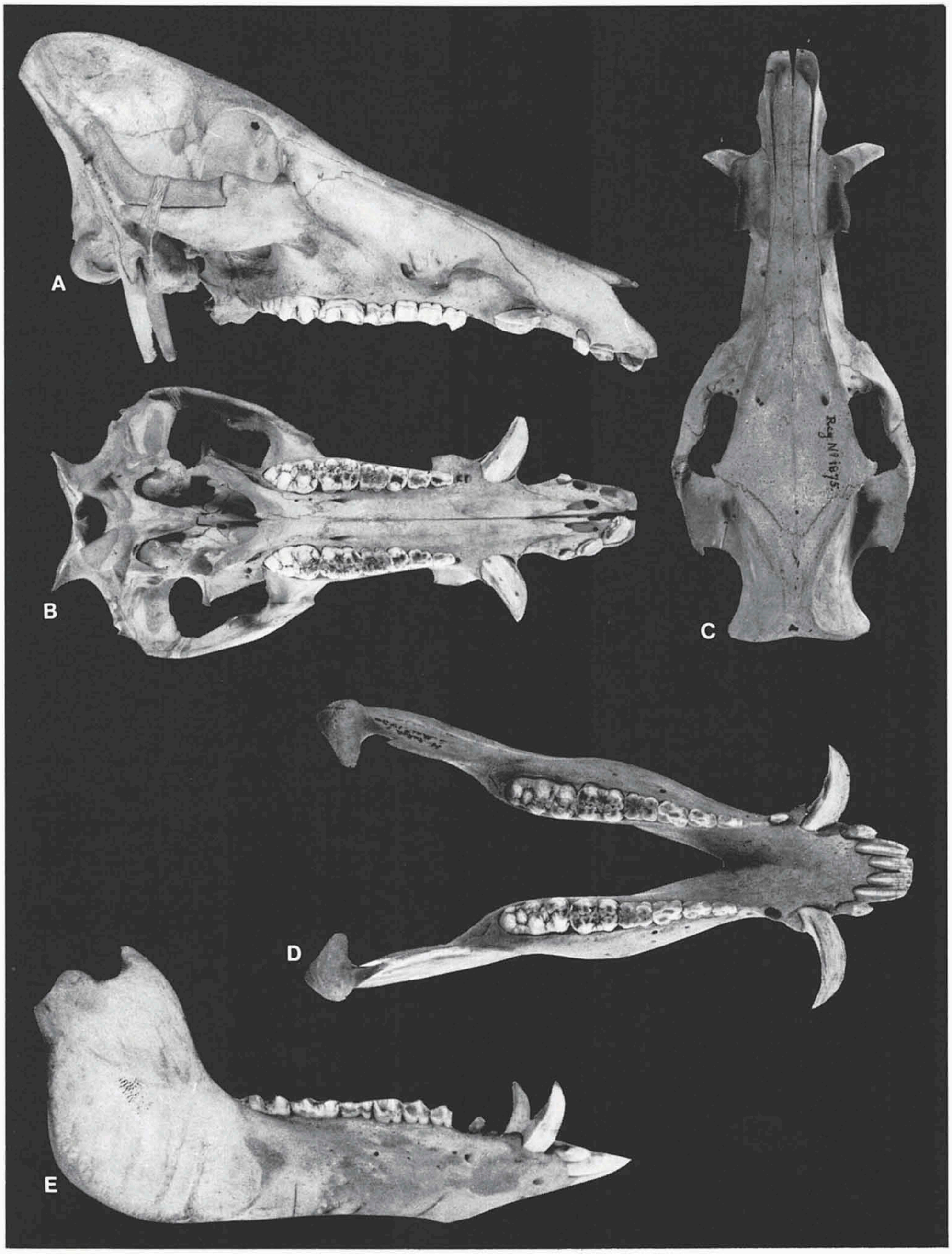
Type — A male skull, RMNH reg. no. 1875.

Type-locality — In the wood (400 m above sea-level) near Pota, a village on the Manggarai Plain, in the western part of the Island of Flores.

Diagnosis — A small species of *Sus* of verrucosic type. The new species is smaller than *Sus celebensis* and *Sus verrucosus*, but the orbit is relatively larger (see Tables 13-14; Figs. 19-22). The profile of the skull is less concave than that of *Sus celebensis* and is more like *Sus verrucosus* in this respect. The dental morphology resembles that of *Sus celebensis*.

Description of the type specimen — The ramus of the lower jaw is inflated, the infra-orbital foramen is diveded by a septum just as in the type specimen of *Sus verrucosus* from

Plate 9



Sus heureni sp. nov.
Pota, Island of Flores.
Fig. A. Skull of adult male, holotype, RMNH 1875, lateral view, approx. × 0.30.
Fig. B. Idem, ventral view, approx. × 0.30.
Fig. C. Idem, ventral view, approx. × 0.30.
Fig. D. Mandible, holotype, RMNH 1875, top view, approx. × 0.30.
Fig. E. Idem, lateral view, approx. × 0.30.

Table 13. Measurements of eleven skull characters of *Sus heureni* sp. nov., coll. RMNH and MZB (for an explanation of the character numbers see Table 7).

Cat.no.	1	2	3	4	5	6	7	8	9	10	11
MZB 8382	287.0	106.5	126.0	—	66.0	107.0	22.0	32.0	33.0	29.3	179.5
MZB 479	290.0	104.0	135.0	—	77.6	112.0	24.6	32.8	31.7	29.5	176.0
RMNH 1875	280.0	104.0	121.2	108.0	68.0	101.0	23.3	34.0	30.3	26.4	164.0
n	3	3	3	1	3	3	3	3	3	3	3
min.	280.0	104.0	121.2	—	66.0	101.0	22.0	32.0	30.3	26.4	164.0
max.	290.0	106.5	135.0	—	77.6	112.0	24.6	34.0	33.0	29.5	179.5
$\bar{x}$	285.7	104.8	127.4	108.0	70.5	106.7	23.3	32.9	31.7	28.4	173.2
log$\bar{x}$	2.46	2.02	2.11	2.03	1.85	2.03	1.37	1.52	1.50	1.45	2.24

Table 14. Measurements of seven mandible characters of *Sus heureni* sp. nov., coll. RMNH and MZB (for an explanation of the character numbers see Table 1).

Cat. no.	1	2	3	4	5	6	7
$\bar{x}$	205.2	93.8	38.1	23.9	52.4	78.1	25.7
log$\bar{x}$	2.31	1.97	1.58	1.38	1.72	1.89	1.41

Java. The canine flange is smaller than that of *Sus verrucosus*, but larger than in *Sus timorensis*. The jugal bone is only slightly inflated just as in *Sus celebensis*. The profile of the skull is less concave, almost straight, and closer to that of *Sus verrucosus*. the posterior part of the horizontal palatine bone ends close to the M^3. The basihyoid is longer and almost the same as in *Sus verrucosus*. P^2, P^2 and P^4 have a pronounced stylus, likewise P_3, P_3 and P_4 have also pronounced stylids, which is a typical character of the verrucosic suid group (see Table 13).

Remarks — By studying the lables of the type specimen, the conclusion was reached that the skull was first (no date) identified as *Sus floresianus* (a scrofic group). This identification was obviously influenced by the fact that the specimen was collected from the Island of Flores where the above species is native. But it is clear that the specimen does not have the scrofic characteristics. Later (no date) Dr van Heuren reidentified the specimen as *Sus celebensis*. The identification shows that van Heuren was aware of the fact that in morphology and size this skull is more related to *Sus celebensis*. However, since there are clear differences in the morphology, I consider the pig of Flores to be a distinct species, which is corroborated by the fact that the Island of Flores was separated from Sulawesi (Celebes) a long time ago.

Sus timorensis Müller & Schlegel, 1845

Sus timorensis Müller & Schlegel, 1845.
Sus timorensis, Jentink, 1905.
Sus verrucosus timorensis, Schwarz, 1914.

Type — A young female skull, cat. Ost. a, RMNH.

Table 15. Measurements of three skull characters of a subadult specimen of *Sus timorensis*, coll. RMNH (for an explanation of the character numbers see Table 7).

Cat. no.	1	3	11
w	209.5	95.3	123.5
e	164.3	74.4	97.5
x	228.0	108.7	149.5
d	225.0	94.2	140.0
a	233.0	102.8	141.0
b	188.7	85.6	110.8
j	250.0	108.0	144.0
v	219.0	99.8	130.8
u	212.2	94.5	125.0
n	9	9	9
min.	164.3	74.4	97.5
max.	250.0	108.7	149.5
$\bar{x}$	214.4	95.9	129.1
log$\bar{x}$	2.33	1.98	2.11

Type-locality — Pritti, near Kupang, Timor.

Revised diagnosis — Small pig, the skull of which is smaller than that of *Sus celebensis* and *Sus heureni* (see Table 15; Fig. 20). The parietal crest is very narrow (9 mm). The dentition of the upper jaw and lower jaw resembles more the verrucosic type than the scrofic type. The stylus of P^3 and stylid of P_3 and P_4 have a verrucosic-type morphology.

Measurements and remarks — There is no adult specimen of *Sus timorensis* in the National Museum of Natural History, Leiden. The type specimen is a semi-adult skull. Since the M^3 is already visible in the alveole, the skull can be considered to be full-grown. The crest is narrow: 9 mm. The length of the skull is 230 mm. According to Jentink *Sus timorensis* has a certain affinity with *Sus vittatus*. But according to the morpholgy of the teeth, the stylus of the praemolars, this species is closer to *Sus verrucosus*, and must be classified in the verrucosic group. Schwarz (1914) placed it as a subspecies in *Sus verrucosus*.

Sus scrofa scrofa Linnaeus, 1758

Sus scrofa Linnaeus, 1758.
Sus scrofa, Lydekker, 1915 (cum syn.).
Sus scrofa, Ellerman & Morrison-Scott, 1951.
Sus scrofa, Ellerman & Morrison-Scott, 1955 (cum syn).

Type — Stored in the Muséum National d'Histoire Naturelle, Paris.

Type-locality — Germany, exact locality unknown.

Diagnosis — The size is moderate to very large; the face is without wart, and the snout relatively short. The lower canine of the male is of the scrofic type. The last upper molar is elongated, with a distinct third ridge. The general colour is brown, with an individual tendency to become blackish. The face, cheeks and throat show greyish white hairs, and the bristles on the nape are long but never form a crest. The colouration of the young is brown, with blackish stripes (see also Lydekker, 1915, p. 310).

Range — Eurasia; in Asia it is distributed eastwards as far as the Island of New Guinea and some other islands nearby (see also Ellerman & Morrison-Scott, 1955).

Sus scrofa vittatus Müller & Schlegel, 1845
Pl. 10.

Sus vittatus Müller & Schlegel, 1845.
Sus vittatus Jentink, 1905.
Sus vittatus vittatus, Lydekker, 1915.
Sus scrofa, Ellerman & Morrison-Scott, 1955.
Sus scrofa vittatus, Hoogerwerf, 1970.

Type — A male skull, cat. Ost. c, RMNH.

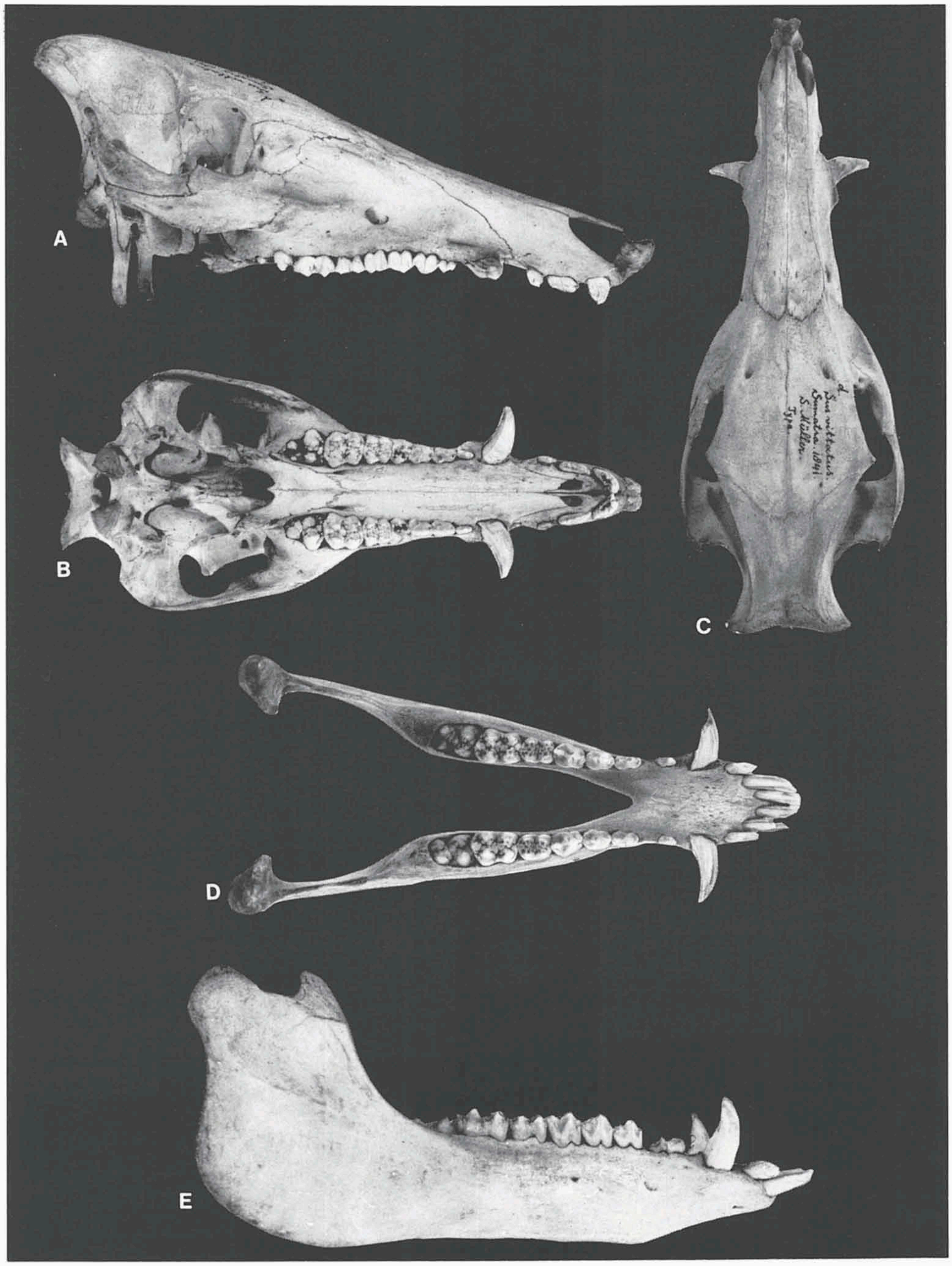
Type-locality — Padang, Sumatra.

Revised diagnosis — Extant pigs of Sumatra. The young has alternate black and reddish brown bands along the sides of the body. The bands vanish with advancing age. The line along the spine is black, and long bristles are present towards the neck. Warts, protuberances or tufts of bristles, such as present of the head of *Sus barbatus* and *Sus verrucosus*, are not developed in *S. s. vittatus*. The skull is more compact, relatively higher and shorter than in *S. barbatus* and *S. verrucosus*. The lower jaw is also higher. Palatine does not extend backwards as in *S. verrucosus*. The length of M_3 is smaller than in *S. verrucosus*. The profile line of the skull is straight or convex. The orbit is larger than in *Sus verrucosus*. The facial crest is pronounced, but no real cresta is present. The well-developed canine is of the scrofic type.

Remarks — *Sus scrofa vittatus* is an extant pig from Indonesia which has a very wide ecological distribution (Hoogerwerf, 1970). In Sumatra it ranges from the coastline up to the mountains. The skull is smaller and shorter than in *Sus verrucosus* and *Sus barbatus*, but larger and longer than in *Sus celebensis* (see Fig. 22). As noted before, in *Sus scrofa vittatus* the male lower canine is of the scrofic type. The morphology of the male lower canine matches the morphology of P^3, which has no or only slightly developed stylus. Also P_3 and P_4 have no clearly developed stylids. In *Sus verrucosus, Sus celebensis* and *Sus barbatus* the stylus and stylids are strongly developed. The ramus of *S. s. vittatus* is thinner than in the lower jaw of *Sus verrucosus*, but it is not very different from that of *Sus barbatus*.

Measurements — The measurements of *Sus scrofa vittatus* are relatively variable (see Tables 16-17). The average length of the skull is 353.3 mm.

Plate 10



Sus scrofa vittatus Müller & Schlegel, 1845
Padang, Sumatra; Recent.
Fig. A. Skull of adult male, holotype, cat. Ost. d, lateral view, approx. × 0.24.
Fig. B. Idem, ventral view, approx. × 0.24.
Fig. C. Idem, dorsal view, approx. × 0.24.
Fig. D. Mandible of adult male, holotype, cat. Ost. d, top view, approx. × 0.24.
Fig. E. Idem, lateral view, approx. × 0.24.

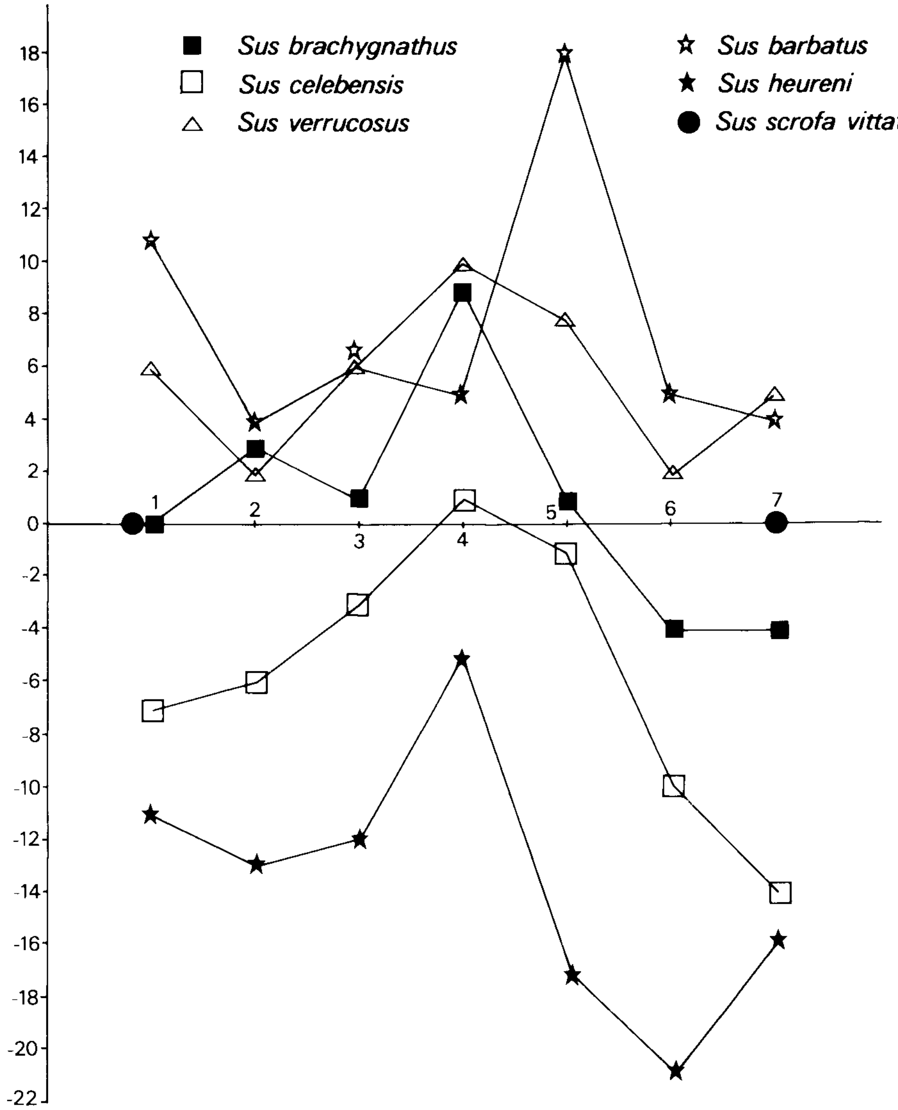
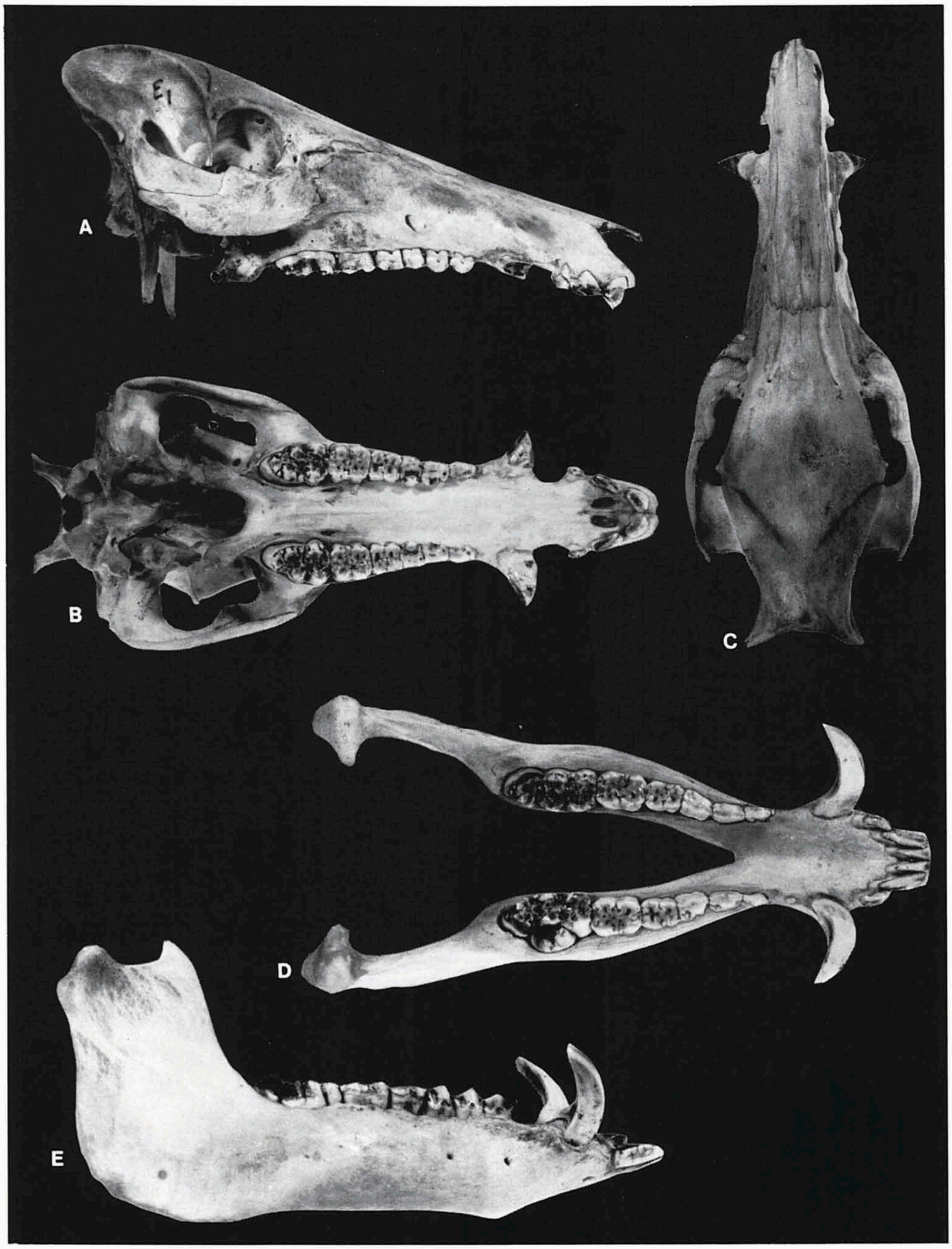


Fig. 22. Diagram showing the differences (× 100) of the logarithms of the mean of the measurements of the lower jaw of *Sus brachygnathus, Sus celebensis, Sus verrucosus, Sus heureni,* and *Sus scrofa vittattus* compared with *Sus scrofa vittatus*.
1 – length of lower jaw; 2 – height of lower jaw; 3 – height of ramus; 4 – thickness of ramus; 5 – length of symphysis; 6 – length of P_2-M_3; 7 – length of M_3.

Sus scrofa milleri Jentink, 1905
Pl. 11.

Sus milleri Jentink, 1905.
Sus vittatus milleri, Lydekker, 1915.
Sus cristatus milleri, Chasen, 1940.
Sus scrofa, Ellerman & Morrison-Scott, 1955.
Sus scrofa milleri, Hoogerwerf, 1970.

Plate 11



Sus scrofa milleri Jentink, 1905
Java, exact locality unknown; Recent.
Fig. A. Skull of adult male, cat. j, lateral view, approx. × 0.26.
Fig. B. Idem, ventral view, approx. × 0.26.
Fig. C. Idem, dorsal view, approx. × 0.26.
Fig. D. Mandible of adult male, cat. j, top view, approx. × 0.26.
Fig. E. Idem, lateral view, approx. × 0.26.
Remark: an abnormal right M_1.

Table 16. Measurements of eleven skull characters of *Sus scrofa vittatus*, coll. RMNH (for an explanation of the character numbers see Table 7).

Cat. no.	1	2	3	4	5	6	7	8	9	10	11
1213	332.3	122.0	137.0	111.3	64.8	—	29.0	38.4	38.0	26.0	206.0
Ost. i	339.3	138.6	141.5	124.6	59.0	113.0	30.0	36.2	34.6	27.9	206.0
Jacob. Mer.	343.2	132.0	145.7	—	72.7	112.5	30.0	38.8	38.2	26.2	213.0
1198	351.0	133.7	148.3	125.4	69.8	109.7	33.4	37.2	35.8	28.0	212.0
ost. h	352.0	141.0	141.0	118.0	69.6	110.0	32.3	38.1	39.2	28.0	207.0
1201	352.5	135.5	146.4	132.5	70.4	110.3	33.0	41.3	42.6	26.5	208.2
3975	354.6	143.2	149.8	130.0	64.6	111.8	30.2	38.0	37.8	27.0	214.0
Ost. c	377.0	141.5	149.0	—	74.5	118.0	35.5	37.0	38.5	31.2	230.6
872	378.0	140.0	146.1	119.0	72.8	114.2	36.0	38.5	49.5	26.5	206.8
n	9	9	9	7	9	8	9	9	9	9	9
min.	332.3	122.0	137.0	111.3	59.0	109.7	29.0	36.2	34.6	26.0	206.0
max.	378.0	143.2	149.8	132.5	74.5	118.0	36.0	41.3	49.5	31.2	230.6
$\bar{x}$	353.3	136.4	145.0	123.0	68.7	112.4	32.2	38.2	39.4	27.5	211.
log$\bar{x}$	2.55	2.13	2.16	2.09	1.84	2.05	1.51	1.58	1.60	1.44	2.33

Table 17. Measurements of seven mandible characters of *Sus scrofa vittatus*, coll. RMNH (for an explanation of the character numbers see Table 1).

Cat. no.	1	2	3	4	5	6	7
872 b	255.0	127.5	52.0	32.3	78.5	111.0	37.3
i 1883	235.0	114.4	44.6	—	57.8	103.7	34.5
872 a	246.0	106.0	46.7	27.0	80.2	108.2	34.0
3975	246.7	129.5	47.0	25.3	63.4	113.4	37.1
Jacob. Mer.	247.6	114.0	44.3	—	69.5	107.7	36.0
n	248.6	121.2	45.6	24.5	66.0	112.0	34.3
1201	260.5	112.9	30.0	30.5	92.0	105.3	35.2
1836	267.0	120.5	45.0	29.0	77.0	117.6	37.7
n	9	9	9	7	9	9	9
min.	235.0	106.0	30.0	24.5	57.8	103.7	34.0
max.	267.0	129.5	52.0	32.3	92.0	117.6	37.7
$\bar{x}$	251.1	118.6	44.3	27.6	72.8	109.7	35.7
log$\bar{x}$	2.40	2.07	1.65	1.44	1.86	2.04	1.55

Type — A male skull, cat. Ost. j, RMNH.

Type-locality — Java, exact locality unknown.

Diagnosis — Wild pig of Java. The lower male canine is of the scrofic type. The skull size is smaller than that of *Sus s. vittatus, Sus verrucosus* and there are fewer bristles on the head than in *Sus vittatus*. The snout is shorter than in *Sus scrofa vittatus*.

Description and remarks — Since the skull and the snout are shorter than in *Sus s. vittatus*, the diastema in the lower and upper jaw is also shorter, and the praemaxilla is smaller. The other skull characters are more or less the same as in *Sus scrofa vittatus* (see Table 18 and Fig. 23).

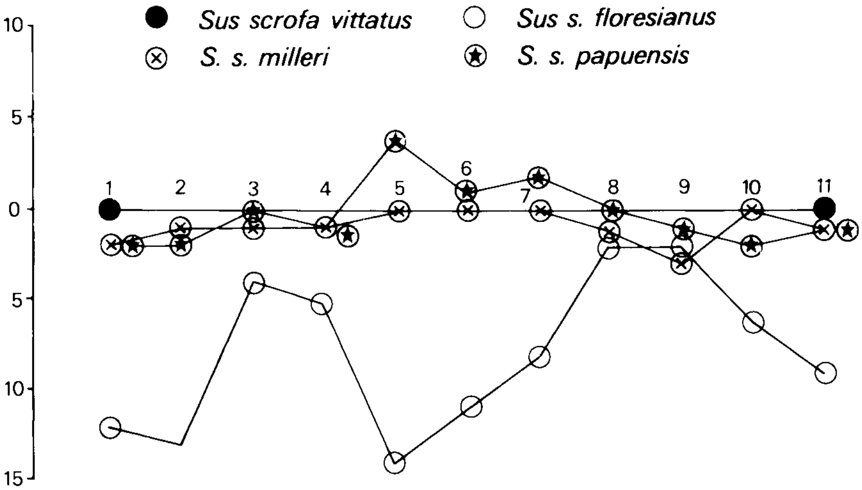


Fig. 23. Diagram showing the differences (× 100) of the logarithms of the mean of the measurements of the skull of *Sus scrofa vittatus, Sus scrofa milleri, Sus scrofa floresianus,* and *Sus scrofa papuensis* compared with *Sus scrofa vittatus*. Same legend as for Fig. 20.

Jentink (1905) named this pig from Java *Sus milleri*, but Ellerman and Morrison-Scott (1955) placed it as a subspecies in the species *Sus scrofa* . The measurements of this subspecies are presented in Table 19.

Sus scrofa floresianus Jentink, 1905
Pl. 12.

Sus scrofa floresianus Jentink, 1905.
Sus vittatus floresianus Lydekker, 1915.
Sus scrofa floresianus, Ellerman & Morrison-Scott, 1955.

Type — A male skull, cat. Ost. a, RMNH 146.

Type-locality — Flores, exact locality unknown.

Diagnosis and description — The skull is smaller (260 mm) than that of *Sus scrofa vittatus* (360 mm). Although it is smaller, it is thick, solid, short, and wide. On the maxillary bone a protuberance is positioned in front of the infra-orbital foramen. The lower male canine is clearly of the scrofic type. The brain case is shorter than in *Sus s. vittatus* but relatively broad. The depression on the facial bone is visible, but not very deep. The facial crest is not very distinct. The lower depression is more pronounced than the upper one. The infra-orbital foramen is larger than that of *Sus s. vittatus*. The canine flange is not very well developed. The eye socket appears to be larger than that of *Sus s. vittatus*. The jugal arch is not inflated and almost the same as in *Sus celebensis*. The palatine is wider at the level of the P^3. The posterior end of the horizontal palatine bone is placed not very far backwards. The foramen magnum has been broken off, and could not be studied. The right infra-orbital foramen is divided by a septum: the posterior part is smaller than the anterior part. Anterior to the infra-orbital foramen there is a strong bony protuberance,

Table 18. Measurements of eleven skull characters of *Sus scrofa milleri*, col. RMNH (for an explanation of the character numbers see Table 7).

Cat. no.	1	2	3	4	5	6	7	8	9	10	11
2664	312.5	123.0	134.0	120.3	58.0	99.0	28.0	38.0	38.2	26.0	189.6
Ost. 1	314.5	121.5	125.5	111.7	—	—	24.8	36.0	35.0	27.0	191.2
1232	337.0	128.5	141.2	111.0	78.8	114.3	34.8	31.2	33.5	27.4	205.3
2662	337.5	127.5	152.3	—	72.0	115.0	33.7	39.2	—	29.5	198.3
2668	342.0	126.5	143.0	119.0	74.8	116.9	30.1	38.5	37.2	26.0	212.0
2663	342.2	130.0	134.3	118.0	63.3	111.0	28.5	37.5	38.0	26.0	205.2
MBU	345.0	—	147.0	127.0	70.8	118.0	38.7	38.7	35.2	27.5	207.7
1186	348.0	136.3	140.0	121.5	61.0	107.5	32.2	37.1	35.4	28.0	213.5
2667	353.8	142.0	140.2	120.3	65.5	107.2	34.2	39.7	39.4	30.6	211.0
2674	356.8	133.2	148.0	122.0	79.9	116.8	41.0	39.0	37.7	28.0	203.0
1924-34	357.0	144.0	150.0	127.5	62.0	119.8	34.0	37.0	38.4	30.0	217.0
2658	359.0	149.0	155.3	128.0	71.2	122.6	32.6	38.2	36.8	26.6	196.0
n	12	11	12	11	11	11	12	12	11	12	12
min.	312.5	121.5	125.5	111.0	58.0	99.0	24.8	31.2	33.5	26.0	189.6
max.	359.0	149.0	155.3	128.0	79.9	122.6	41.0	39.7	39.4	30.6	217.0
$\bar{x}$	342.1	132.9	142.6	120.6	68.8	113.5	32.7	37.5	36.8	27.7	204.2
log$\bar{x}$	2.53	2.12	2.15	2.08	1.84	2.05	1.51	1.57	1.57	1.44	1.31

Table 19. Measurements of eleven skull characters of *Sus scrofa papuensis*, coll. RMNH (for an explanation of the character numbers see Table 7).

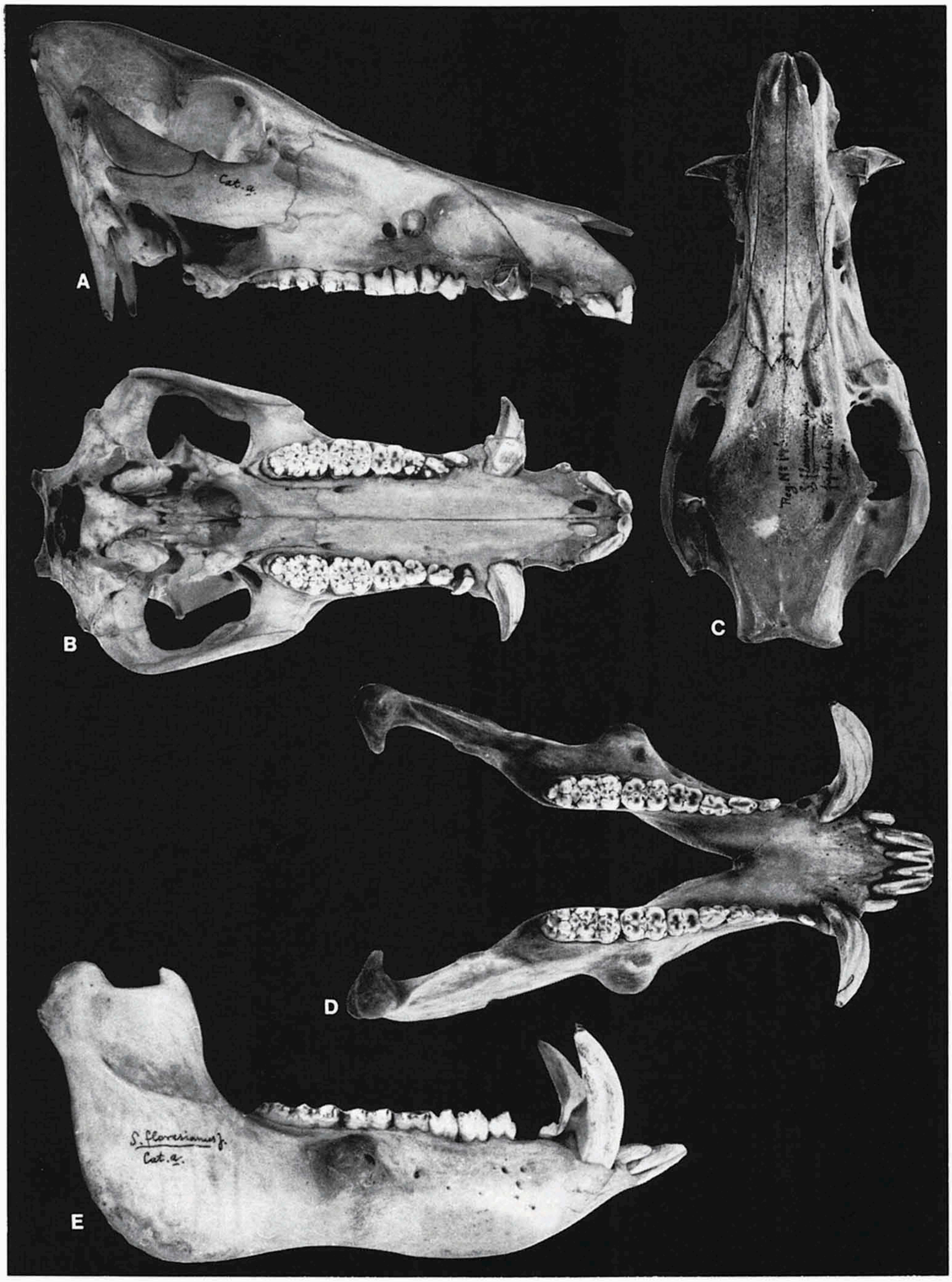
Cat.no.	1	2	3	4	5	6	7	8	9	10	11
VSpD i	304.0	117.6	139.8	120.0	70.0	111.0	28.0	35.5	39.0	28.1	185.2
CKA	315.7	125.0	142.3	130.0	69.2	—	30.7	37.4	37.1	28.8	193.4
VNG 9211	331.0	127.0	144.0	123.0	69.4	—	33.8	37.7	38.8	—	200.5
20550	332.2	124.3	136.0	119.0	71.7	113.0	33.5	37.7	37.6	22.6	202.2
CK 1923	337.0	126.0	138.8	117.5	81.5	114.6	34.5	39.5	35.1	25.5	198.0
475	345.0	127.6	146.5	127.8	80.6	115.7	34.8	40.0	38.8	26.0	211.9
K 1923	351.0	138.8	146.8	126.0	72.4	122.0	32.7	36.4	35.5	27.1	210.7
NG 8	363.7	142.3	151.5	130.0	81.5	123.5	39.0	38.5	40.0	23.6	218.0
NGE 1907	372.5	137.5	150.6	145.0	82.0	—	39.0	37.0	—	—	221.1
n	9	9	9	9	9	6	9	9	8	7	9
min.	304.0	117.6	136.0	117.5	69.2	111.0	28.0	35.5	35.1	22.6	185.2
max.	372.0	142.3	151.5	145.0	82.0	123.5	39.0	40.0	40.0	28.8	221.1
$\bar{x}$	339.1	129.5	144.0	126.5	75.4	116.6	34.0	37.7	37.7	26.0	204.6
log$\bar{x}$	2.53	2.11	2.16	2.10	1.88	2.07	1.53	1.58	1.58	1.41	2.31

which is however absent is the skull of a female specimen. The profile is concave at the posterior end at the nasal bone. The dentition is of the scrofic type: the stylus and stylids of the praemolars are hardly visible. The first praemolars are absent. The lower jaw is short, and strongly built. The buccal sides of the left and the right ramus show a bony protuberance which is more pronounced than the protuberance on the maxillas. The lower canine is strongly developed and shows the scrofic type morphology.

The measurements of this species are presented in Tables 20-21.

Remarks — Lydekker (1915) considered the form from Flores to be a subspecies of *Sus vittatus* and refers to it as *Sus vittatus floresianus*. As Ellerman and Morrison-Scott (1951,

Plate 12



Sus scrofa floresianua Jentink, 1905
Flores, exact locality unknown; Recent.
Fig. A. Skull of adult male, holotype, RMNH 146 (cat. Ost. a), lateral view, approx. × 0.31.
Fig. B. Idem, ventral view, approx. × 0.31.
Fig. C. Idem, dorsal view, approx. × 0.31.
Fig. D. Mandible of adult male, holotype, RMNH 146 (cat. Ost. a), top view, approx. × 0.31.
Fig. E. Idem, lateral view, approx. × 0.31.

Table 20. Measurements of fourteen skull characters of *Sus scrofa floresianus*; cat. Ost. a, RMNH 146.

Skull character	x	log x
length of skull	271.0	2.43
length of hind skull	101.0	2.00
width of parietal crest	28.0	1.43
width of skull	132.7	2.12
width of skull at anterior orbit	109.0	2.04
width of occipital	50.0	1.70
height of foramen magnum-occipital crest	88.0	1.94
width of jugal	26.7	1.43
width of eye (horizontal)	36.2	1.56
height of eye (vertical)	37.4	1.57
length of basioccipitosphenoid	24.0	1.38
length of palatine	168.6	2.23
length of P^1-M^3	88.6	1.95
length of M^1-M^3	59.2	1.77

Table 21. Measurements of seven mandible characters of *Sus scrofa floresianus*; cat. Ost. a, RMNH 146.

length of ramus	200.3	2.30
height of gonion (condyle-gonion ventral)	165.0	2.22
height of ramus at M_1	45.3	1.66
thickness of ramus	25.0	1.40
length of symphysis	63.0	1.80
length of P_2-M_3	92.0	1.96
length of M_1-M_3	62.0	1.79

1955) synonymised *scrofa* and *vittatus* the pig from Flores of the scrofic type would be called *Sus scrofa floresianus*.

Sus scrofa papuensis Lesson & Garnot, 1826
Pl. 13.

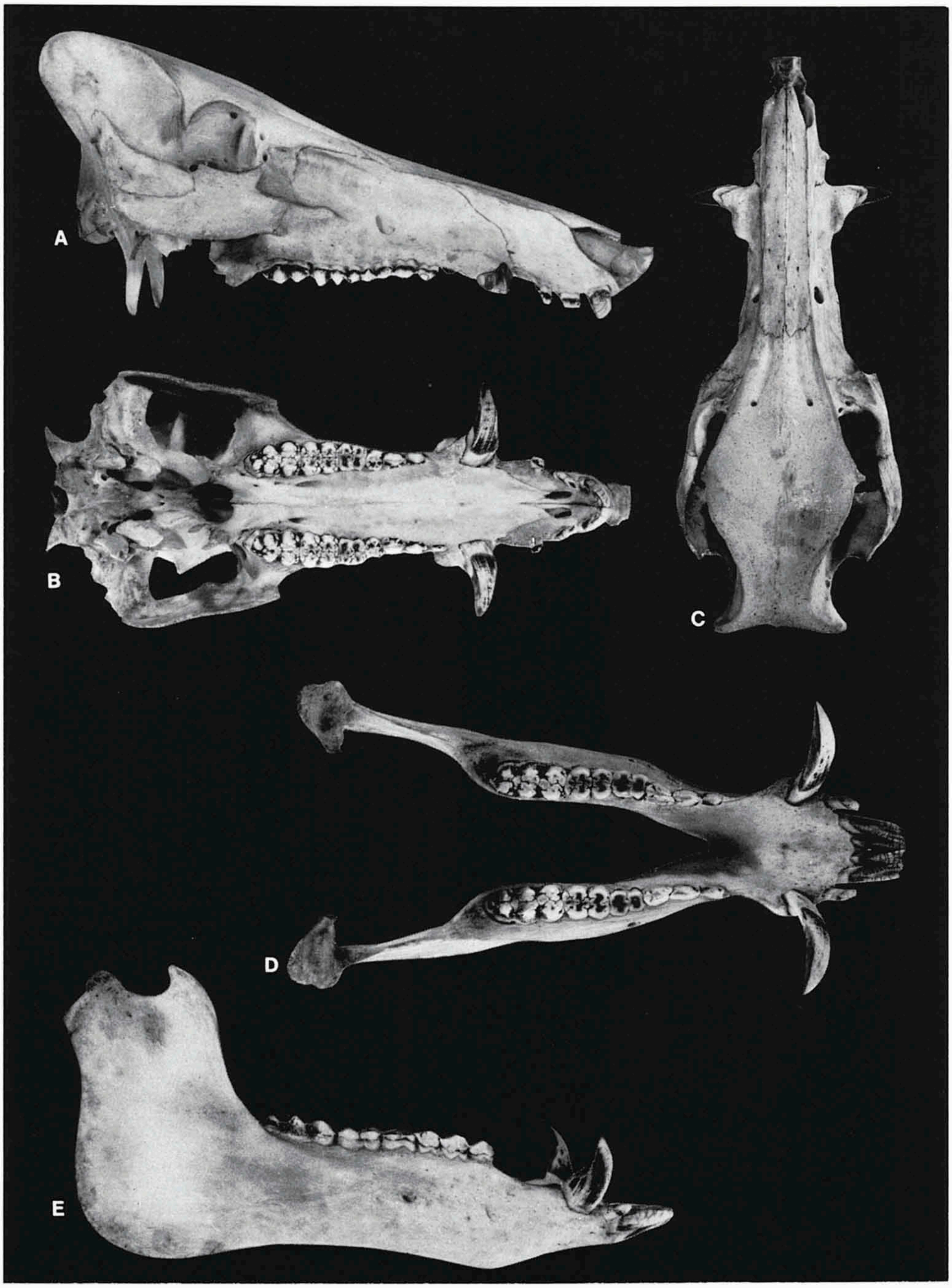
Sus papuensis Lesson & Garnot, 1826.
Sus papuensis, Jentink, 1905.
Sus papuensis, Lydekker, 1915.
Sus niger, Jentink, 1905, part.

Type — Stored at the Muséum National d'Histoire Naturelle, Paris.

Type-locality — Irian (New Guinea), exact locality unkown.

Remarks — The measurements of this pig are presented in Table 2. This species is smaller than *Sus scrofa vittatus*. The male lower canine is of the scrofic type. The profile line of the skull is concave at the base of the nasalia. The width of the orbit is broader than in *Sus verrucosus*, and resembles that of *Sus s. vittatus*. Bony palate ends about 9 mm behind M^3. This pig is very similar to *Sus scrofa* from Sumatra and Java. From Fig. 23 it can be inferred that the variation of *Sus s. papuensis* is similar to that of *Sus s.*

Plate 13



Sus scrofa papuensis Lesson & Garnot, 1826
Irian (New Guinea), exact locality unknown; Recent.
Fig. A. Skull of adult male, RMNH 475, lateral view, approx. × 0.24.
Fig. B. Idem, ventral view, approx. × 0.24.
Fig. C. Idem, dorsal view, approx. × 0.24.
Fig. D. Mandible of adult male, RMNH 475, top view, approx. × 0.24.
Fig. E. Idem, lateral view, approx. × 0.24.

vittatus. Further it can be concluded that *Sus scrofa papuensis* is not very different from *Sus scrofa vittatus* and that the separation into two different species is not justified. This corroborates the opinion of Hoogerwerf (1970), who considered it a subspecies of *Sus scrofa*.

Discussion about the extant representatives of the genus Sus

The various species of *Sus* in the Indonesian Archipelago can be distinguished not only by their external morphology but also by the skull morphology. The distribution pattern of the various species seems somewhat illogical (Fig. 24), but this is probably the result of human activity. Man introduced species of pigs, especially *Sus scrofa*, onto islands where they were not native. *Sus scrofa* was brought to Flores, Timor and possibly also to Ambon and Ceram (Lydekker, 1915, p. 335). At present it is difficult to express the morphological differences in the taxonomical classification (e.g. the difference between *Sus celebensis* and the verrucosic type from Flores). More research, such as cytogenetic studies (e.g. Bosma, 1978), is needed in order to evaluate the morphological differences. The use of the name *Sus verrucosus* for all the various forms masks information which is needed for zoogeographical reconstruction. For example, *Sus celebensis* is clearly smaller than *Sus verrucosus* and so are the pigs of Flores and Timor, and consequently in the literature the name *celebensis* is often attached to the small forms of Flores and Timor. The morphological differences, as reported in this study, should be reflected in the taxonomy at the specific level concerning the verrucosic-type suids: from Sulawesi (Celebes) – *Sus celebensis*; from Flores – *Sus heureni*; and from Timor – *Sus timorensis*. The various scrofic-type suids are subdivided at the subspecific level (see also Hoogerwerf, 1970) as a result of geographical isolation caused by the introduction of *Sus scrofa* onto different islands by man (Clason, 1976; Groves, 1981); on Flores – *Sus scrofa floresianus*, and on Irian (New Guinea) and Maluku (Moluccas) – *Sus scrofa papuensis*, since the morphological differences are less clear (see Fig. 23).

Phylogeny, isolation and biostratigraphy

PHYLOGENY

From the description of the fossil suids in the last chapter, we can conclude that they are closely related; this relationship is expressed in their taxonomy, as they are all classified in one genus: *Sus*. Regarding the relation between the fossil and the extant species, von Koenigswald (1933, p. 43) suggested the following (translated): '*Sus brachygnathus*, the smallest species of our group, shows so many similarities with *Sus celebensis* that we do not doubt that the specimens described by Stremme were the same as the species described by Dubois'. And further on (p. 49): '*Sus terhaari, Sus verrucosus* and *Sus barbatus* probably have the same ancestor'. This statement is based mainly on the elongation of the molars of these three species. Dubois pointed to the similarity between *Sus macrognathus* and *Sus verrucosus*. Their morphology is very similar, and it is impossible to distinguish between apomorph and plesiomorph characters. Therefore conclusions concerning the phylogenetic relationships of the various taxa must be rather speculative.

Island / Species	*Sus barbatus*	*Sus verrucosus*	*Sus celebensis*	*Sus heureni*	*Sus timorensis*	*Sus scrofa*
Sumatra	×	×				×
Kalimantan (Borneo)	×					?
Java		×				×
Sulawesi (Celebes)			×			?
Flores				×		×
Timor					×	×
Ceram, Ambon (Moluccas)					?	×
Irian (New Guinea)					?	×

Fig. 24. Distribution of extant representatives of the genus *Sus* on various islands of the Indonesian Archipelago.

Palaeogeography changed drastically several times during the Pleistocene (van Bemmelen, 1949; Sondaar, 1981) and it is quite possible that a population of suids became isolated in a certain area, but after some time could spread out again.

The taxonomy proposed in this paper differs from that of von Koenigswald (1933). In this paper it is concluded that *Sus terhaari* differs from *Sus macrognathus* only at subspecific rank. The author agrees with von Koenigswald that *Sus macrognathus terhaari* might be the ancestor of *Sus verrucosus*, but disputes the opinion that *Sus celebensis* is identical with *Sus brachygnathus* in view of the differences in skull morphology. *Sus celebensis* is considered to be a locally evolved species, of which *Sus macrognathus* or *Sus verrucosus* was the ancestor.

When speculating on the phylogeny one has to take into account the data concerning the biostratigraphic succession (see Fig. 27). Far-reaching conclusions cannot be drawn on the basis of the Kaliglagah material as the material is too limited. The M^3 of the so-called *Sus stremmi* (von Koenigswald, 1934) is clearly larger than that of *Sus brachygnathus*. If the upper M^3 figured by von Koenigswald is really an M^3 (as stated before it is probably an M_3), then this molar is very elongated. There are no indications that *Sus brachygnathus* is a descendant of this species (if a valuable species at all!) and it is probable that *Sus brachygnathus* is an immigrant. The difference between *Sus brachygnathus* from Trinil (type locality) and *Sus brachygnathus* from Bangle is that the dental elements from the latter locality are slightly larger (see Fig. 12). In Bangle *Sus macrognathus* is present as well. The relationship between this species and the former species is not clear. Two possibilities can be considered: (1) *Sus brachygnathus* is ancestral to *Sus macrognathus*; (2) *Sus macrognathus* evolved somewhere outside Java and immigrated together with several other new faunal elements, as are present in Kedungbrubus (de Vos et al., 1982). The first possibility seems the more logical one since *Sus brachygnathus* is morphologically very close to *Sus macrognathus* and also because neither species has been reported from outside Java.

Palaeogeographically it is quite possible that a small population of *Sus brachygnathus* became isolated on Java during an interglacial period, evolved into *Sus macrognathus*, which later, during a glacial period, was able to spread over Java (allopatric evolution model). However, a sympatric evolution model, based on differences in behaviour is also a possible explanation. Leinders (1977) demonstrated that changes in

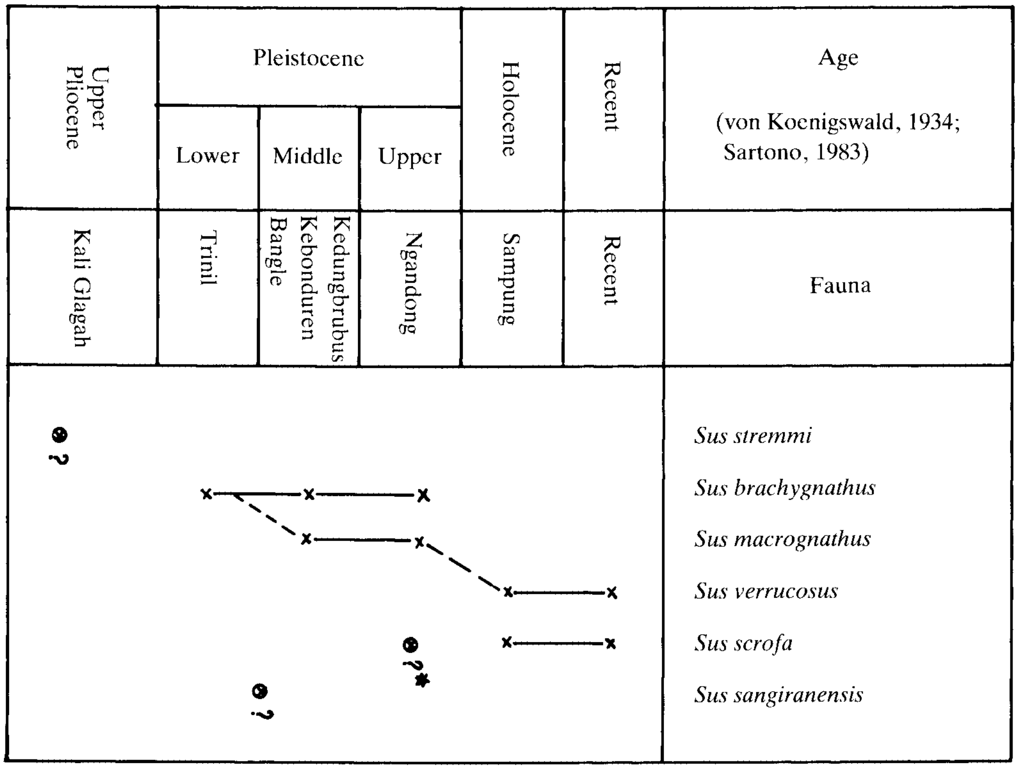


Fig. 25. Phylogeny of the genus *Sus* on Java: × –first occurrence; * – von Koenigswald mentions this species from Ngandong, but the material on which his identification is based is too fragmentary for identification at species level; arrows indicate direct relationships.

behaviour precede and induce changes in morphology. The presence of two closely related species is quite possible, as is demonstrated by the two extant species on Java and Sumatra. In the Ngandong fauna the two fossil species are both represented. I favour the supposition that *Sus verrucosus* evolved from *Sus macrognathus*. This is based on the morphological similarities. The arrival of *Sus scrofa vittatus* and *milleri* probably caused the extinction of *Sus brachygnathus*. In the late Pleistocene or Holocene *Sus scrofa* was most probably introduced by man. *Sus celebensis, Sus heureni* and *Sus timorensis* probably evolved from the *verrucosus* group.

It is not known when *Sus* first appeared on Sulawesi (Celebes) and Timor. A fossil or subfossil specimen of *Sus celebensis*, without exact locality data, was described by Hooijer (1969). So far no *Sus* fossils have been described from the Pleistocene of Flores and Timor. The arrival of *Sus* on these islands must have been a relatively recent event. Theoretically it is possible that *Sus brachygnathus* was the ancestor of *Sus celebensis*, although the proportions of the skulls are different. It seems more probable that the ancestor was closely related to *Sus verrucosus* because (1) the first occurrence of *Sus celebensis* seems to be after the extinction of Sus brachygnathus; and (2) the morphology of the skull is closer to that of *Sus verrucosus* than to that of *Sus brachygnathus*.

Sus scrofa floresianus is clearly a dwarf relative of *Sus scrofa vittatus*. On Flores there is yet another species which is related to the *verrucosus* group. We see the same picture in Timor: here there are also two species, both of them small. One belongs to the *scrofa* group, the other is related to *Sus verrucosus*. The first one, *Sus scrofa*, is generally considered to be a wild descendant of the domesticated pig (Schwarz, 1914). The one close to *Sus verrucosus*, *Sus timorensis*, is the original form from the island. Perhaps we can explain the presence of two forms on Flores in the same way. *Sus scrofa floresianus* may represent the wild form of the domesticated *Sus scrofa* of Flores (introduced by man), whereas the other (*Sus heureni*) is the original form from the island.

ISOLATION AND ITS INFLUENCE ON SUID EVOLUTION

From Sulawesi (Celebes) two endemic genera of the Suidae have been described: the fossil *Celebochoerus* and the extant *Babyrousa*. Fossil material of endemic suids is also known from Mediterranean islands, for example from the Pliocene/Pleistocene of Sardinia. In these examples the endemism is at the genus level and it is evident that isloation played an important role in the evolution of those genera (Sondaar, 1977).

The effect of isolation is perhaps less clear in the suids from Java and the Lesser Sunda Islands, since no endemic genus evolved, and the endemism is at the species level. One of the main aspects in this process is the size reduction that occurs on islands such as Flores, Timor and Sulawesi. The reduction in size of these suids in a relatively short period most probably represents an adaptation to island life. There seems to be a correlation between the size of the pig and the size of the island. Hooijer (1949, p. 128) states that since the time of their immigration into the Greater Sunda Islands (in the late Pliocene or in the early Pleistocene) various species have undergone a gradual diminution in size, accompanied in some cases by essential changes in the structure of their limbs or feet. What we see in the genus *Sus* on Java is not in accordance with this statement. *Sus stremmi* is big compared to the younger form. The earlier forms of *Sus brachygnathus* are smaller than the later forms of *Sus brachygnathus*. In *Sus macrognathus* too we can see that there was an increase in size during the Pleistocene (this is very well demonstrated by a comparison of *Sus macrognathus* from Kedungbrubus and the one from Ngandong). However, from Late Pleistocene onwards a decrease in size can be demonstrated. This could be correlated with the diminution in size of Java during the Holocene, during which period the sea level rose c. 140 m (Orchistan, 1979). The morphological changes have not yet been sufficiently documented by fossil material for a detailed study of this process to be made. A detailed study of more material as well as a functional analysis of the post-cranial morphology of the small forms from the Lesser Sunda Islands could give us more information about the effect of isolation on the evolution of suids. At this moment we can assume that there is a correlation between the size of an island and that of the suid inhabiting the island. However, we should bear in mind that on the smaller of the Lesser Sunda Islands there were no large carnivores, like tigers. This factor probably played an important role too, although it apparently has not affected the diminution is size of the suids on Java since the late Pleistocene, since the tiger was well represented on this island, even during the Holocene.

BIOSTRATIGRAPHIC USE OF *SUS* ON JAVA

The differences in the faunal composition of Trinil and Kedungbrubus are summarized in Fig. 25. The faunal succession according to de Vos et al. (1982) is presented in Fig. 26, and the succession according to Sartono (1983) in Fig. 27. These new ideas concerning the faunal succession corroborate the data on the age of the Mojokerto localtiy as reported by Sartono et al. (1981).

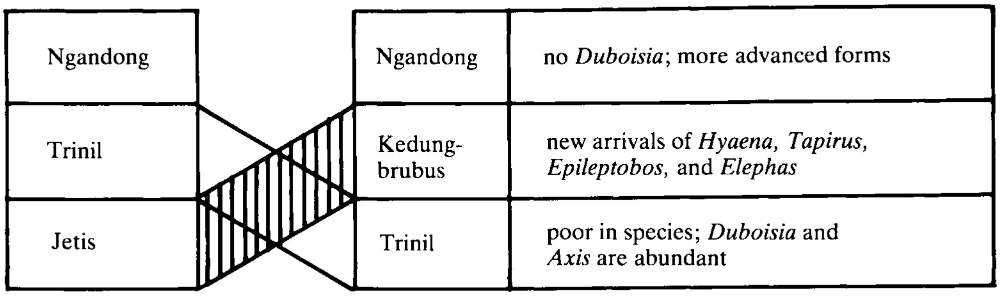


Fig. 26. Faunal succession on Java during the Pleistocene (de Vos et al., 1982): A – after von Koenigswald, 1934; B –proposed in this paper; C – the main faunal composition.

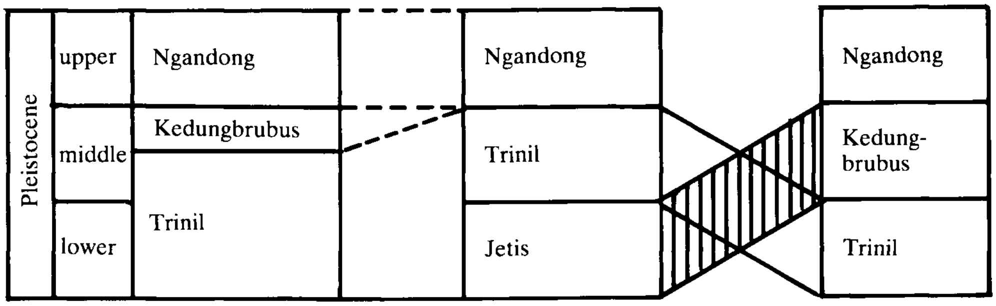


Fig. 27. Pleistocene faunal succession of Java (after Sartono, 1983): A – von Koenigswald, 1934; B – de Vos et al., 1982; C – proposed in this paper. Correlation between A-B made by de Vos et al. (1982), and between A-C proposed by the author in this paper.

At first sight the suids seem to be less suitable for use in biostratigraphy, especially when one considers the scatter diagram from Sangiran (Figs. 16-17). In this case, however, material from different localities and different stratigraphic levels was mixed, resulting in a large homogeneous cluster. However, if we consider the localities separately some clear evolutionary trends can be recognised: (1) increase in size, (2) decrease in size, (3) changes in the length/width ratio of M_3, (4) number of species present at one locality (level). These evolutionary trends can be used to construct a biostratigraphic model for the Suidae, such as presented in Fig. 29.

Conclusions

The fossil and Recent material from Indonesia belonging to the genus *Sus* has been revised, using the same morphological characters. As a result, the following fossil (sub)species are recognised (compare Fig. 28): *Sus brachygnathus, Sus macrognathus macrognathus, Sus macrognathus terhaari, Sus celebensis, Sus stremmi,* and *Sus sangiranensis*. The latter two, however, only questionably so because of the limited material available. The Recent material is referred to nine species and subspecies, including a new one: *Sus barbatus, Sus verrucosus, Sus celebensis, Sus heureni* sp. nov., *Sus timorensis, Sus scrofa vittatus, Sus scrofa milleri, Sus scrofa floresianus,* and *Sus scrofa papuensis*.

	(Sub)species									
Skull character	*Sus barbatus*	*Sus verrucosus*	*Sus macrognathus*	*Sus brachygnathus*	*Sus celebensis*	*Sus timorensis*	*Sus heureni*	*Sus scrofa vittatus*	*Sus scrofa floresianus*	
Type of canine	B	B	B	B	B	B	B	A	A	A: scrofic B: verrucosic
Relative length of molar/praemolar	C	C	C	B	B	A	A	B	A	A: short B: average C: long
length of M_3	C	C	C	B	A	A	A	B	A	A: short B: average C: long
Inflation of lower jaw	C	A	B	A	B	B	B	C	C	A: thick B: average C: thin
Ratio of orbit height jugal width	C	A	B	B	B	B	B	C	C	A: big B: average C: small
Type of praemolar	A	A	A	A	A	A	A	B	B	A: stylus pronounced B: stylus not pronounced

Fig. 28. Comparison of six skull and mandible characters of nine species and subspecies of the genus *Sus* in Indonesia.

Fauna	Species
Ngandong	*Sus brachygnathus* *Sus macrognathus* (larger than the species from Kedungbrubus and Bangle)
Kebonduren Kedungbrubus Bangle	*Sus macrognathus* *Sus brachygnathus* (larger than the species from Trinil)
Trinil	*Sus brachygnathus*
Kaliglagah	*Sus* sp. (not well defined) (larger than the species from Trinil)

Fig. 29. Biostratigraphy for the Quaternary of Java, based on the genus *Sus*.

The geographical distribution of the Suidae in Indonesia is as follows (compare Fig. 1):
on Sumatra: *Sus scrofa vittatus, Sus verrucosus* and *Sus barbatus* (all extant);
on Java: *Sus brachygnathus, Sus macrognathus macrognathus, Sus stremmi, Sus sangiranensis* (all fossil), *Sus scrofa milleri*, and *Sus verrucosus* (extant);

on Borneo: *Sus barbatus* (extant);
on Flores: *Sus scrofa floresianus* and *Sus heureni* (both extant);
on Timor: *Sus timorensis* (extant);
on Sulawesi (Celebes): *Celebochoerus heekereni* (fossil), *Sus celebensis* and *Babyrousa babyrussa* (both fossil and extant);
on Irian Djaja (New Guinea): *Sus scrofa papuensis* (extant).

The main evolutionary trends are related to size increase or decrease. The small suids from Sulawesi, Flores and Timor are thought to have resulted from island-evolution. The size increase in *Sus macrognathus* could prove very useful for a more detailed biostratigraphy.

There were clearly niches for two closely related species of *Sus* in the Indonesian archipelago, resembling for example to-days situation of Java and Sumatra. *Sus brachygnathus* probably became extinct after the arrival of *Sus scrofa*, whereas *Sus macrognathus* evolved towards *Sus verrucosus*. The (palaeo)ecological conditions, allowing two closely related suid species to live in the same area, are not clearly understood.

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