PLEISTOCENE VERTEBRATES FROM CELEBES. VIII. DENTITION AND SKELETON OF CELEBOCHOERUS HEEKERENI HOOIJER

by

Dr. D. A. HOOIJER
(Rijksmuseum van Natuurlijke Historie, Leiden)

with pls. I-VI

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INTRODUCTION

The very first Pleistocene vertebrate remains to be made known from the island of Celebes were two fragments of upper canines that I considered to represent a new genus and species of Suidae (Hooijer, 1948a). These specimens, collected by Mr. H. R. van Heekeren at Beru near Tjabengè (Sopeng district), between the Walanae river and the Singkang depression, about 100 km Northeast of Macassar in Southwestern Celebes, have been entrusted to me by the Head of the Archaeological Survey, Prof. Dr. A. J. Bernet Kempers. More and better material soon turned up, and two rather complete upper tusks of *Celebochoerus* were described in 1950 (Hooijer,

1950b). However, this unmistakably new suid remained of uncertain position as the upper canine has not been much used in suilline classification. More so are the lower canines and the premolars.

Now that the entire dentition and many of the limb and foot bones of *Celebochoerus* are available it is possible to revise and to expand the original diagnosis, and to indicate its closest affinities within the pig family.

Celebochoerus heekereni Hooijer is the most common animal in the Pleistocene Tjabengè fauna of Celebes which further contains extinct forms like a gigantic land tortoise, *Testudo margae* Hooijer (1948b), *Stegodon* spec. (Hooijer, 1953b), and a dwarf archidiskodont elephant, *Archidiskodon celebensis* Hooijer (1949a, 1953a, 1953c). Further, extinct races of two living endemic mammals, *Anoa depressicornis* (Smith) and *Babyrousa babyrussa* (L.), have been described (Hooijer, 1948c). The most prolific site discovered by Mr. Van Heekeren is Sompoh, 12 km North of Beru; the fauna of this locality is similar to that of Beru (Hooijer, 1949b). A third locality in the Tjabengè area on the Walanae river, Tjeleko, is 8 km North of Sompoh. The fauna of this site, although not very rich in specimens, contains the same species found at Sompoh and Beru further to the South.

As shown by the matrix adhering to some of the fossil specimens (Hooijer, 1948b, p. 1169; 1949a, p. 205; 1949b, p. 149) the Tjabengè fossils are derived from river-laid sediments with volcanic components, but they have not yet been found in situ. The existence of a flake culture at the same sites that is similar to the Sangiran culture found in the Upper Pleistocene Notopuro beds of Java (Van Heekeren, 1949; Beyer, 1952, p. 23; Tweedie, 1953, p. 74) indicates that we may find fossil Man at Tjabengè some day if and when collecting in the area can be resumed.

Celebochoerus heekereni Hooijer

Celebochoerus heekereni Hooijer, Proc. Kon. Ned. Akad. v. Wetenschappen Amsterdam, vol. 51, 1948, p. 1025, pl. I figs. 1-6; Zool. Med. Museum Leiden, vol. 30, no. 21, 1950, p. 308, pl. XVI figs. 2-3.

? *Babyrousa babyrussa beruensis* Hooijer, Proc. Kon. Ned. Akad. v. Wetenschappen Amsterdam, vol. 51, 1948, p. 1326, pl. I figs. 2-5.

Holotype: base of left upper canine figured in Hooijer (1948a, figs. 1-3).

Locality: Beru, Sompoh, and Tjeleko, near Tjabengè (Sopeng district), about 100 km Northeast of Macassar, Southwestern Celebes.

Age: Pleistocene.

Diagnosis: Incisors as in *Sus* but less hypsodont; enamel of I^1 only one

and one-half higher than wide labially; labial height of enamel of I_{1-2} only two times the width. Lower canines as in *Sus verrucosus* in cross section. Upper canines much wider than the lower ones, subtriangular in cross section, slightly constricted at pulp cavity; anterior surface at right angles to upper surface and slightly narrower than the latter; upper canines projecting more sideways and placed more backward than in *Sus,* the ends extending beyond the lower canines; enamel restricted to one band of variable width at anterior edge below, developed only in less than one-half of the number of specimens. Female canines similar to male but about three-fourths as large in linear dimensions. Two premolars in the mandible, three in the maxillary, shaped as in *Potamochoerus* but less hypsodont; P_3 with strong protoconid, slightly compressed transversely, and talonid one-half as high as protoconid, anterior cingular point small or absent; P_4 with massive and conical protoconid, uncleft at the apex, talonid two-thirds as high as protoconid, anterior point of cingulum one-third as high at most; P^2 small, degenerate; P^3 sectorial with conical paracone, well-developed inner talon and deep but narrow postero-internal fossa; P^4 with paracone and metacone rounded and separated by a distinct cleft, anteroposterior ridge lingually of paracone connected with the latter up to the apex, central fossa narrow, and protocone rounded. Premolars not enlarged relative to molars: P_4 as wide as M_1, and P^3 decidedly less wide than M^1; premolar series slightly diverging to the front. Molars with thick and very weakly folded enamel and no lobe-formation, cusps distinct, transverse valleys wide open; talon to M^3 and talonid to M_3 short. Skull with the zygomatic process of the maxillary springing out rather abruptly from the surface of the cheek, as in *Potamochoerus,* and placed more forward relative to the molars than in *Sus* or *Potamochoerus:* the anterior margin of the orbit above middle of M^3, and facial crest anterior to M^3, as in *Propotamochoerus.* Lateral angulation of anterior frontal and nasal regions absent, as in *Phacochoerus* and *Hylochoerus.* Strong tubular alveolus for upper canine without jugum caninum above. Mandible rather thick, and medial concavity for pterygoid muscle less extended than in *Sus.* Skeleton large and massive; distal articular surface of radius as in *Sus verrucosus;* unciform with obtuse angle between magnum and third metacarpal facets; third metacarpal robust; fifth metacarpal smallish proximally as in recent Suidae.

In dedicating the unique species of *Celebochoerus* to Mr. H. R. van Heekeren I have wished to honour a man, than whom no one would have been better qualified to explore the ancient hunting grounds of South-western Celebes. It is due entirely to his initiative and untiring energy that

the collection described in the present series of papers was built up, and we can only hope that the search for fossil vertebrate material and artifacts can be resumed in the not-too-distant future.

LOWER PREMOLARS

The P_4 of *Celebochoerus* has a strong, conical main cusp (protoconid) without any indication of a secondary cusp. Anteriorly it falls off steeply to the base of the crown where the cingulum usually forms a small point. From the apex of the protoconid a ridge descends backward for one-third of the height of the main cusp, then it continues horizontally backward, and joins the posterior transverse cingulum in the formation of a posterior cusp, the talonid, which is also conical but only two-thirds as high as the protoconid.

In the Celebes collection there are twenty specimens of P_4. Among this material two types can be distinguished, in one of which the crown is widest behind, with a strong transverse posterior cingulum and tapering to the front, and with the cingulum forming a distinct cusp anteriorly. This is the type shown in a left P_3-M_3 from Sompoh, the best sample of the lower dentition available, shown in pl. I figs. 1-2. The other type of P_4 is wider across the base of the protoconid than behind, with the talonid less extended transversely, and the anterior cingular point hardly developed or absent. There are transitional specimens.

The P_4 in the left P_3-M_3 from Sompoh is rather extreme in its width being decidedly greater behind than in front (pl. I fig. 1), the crown thus assuming a trapezoidal outline, and in the heavily developed posterior cingulum. The ridge descending backward from the protoconid is slightly worn, and so is the talonid cusp. There is one broad root anteriorly, and there are a transverse pair of roots behind. On the anterior slope of the protoconid a weak ridge is seen to connect the apex with the anterior cingular elevation, almost completely hidden below the talonid of the P_3, that is one-third as high as the main cusp.

An almost unworn and perfectly preserved specimen of P_4 (pl. II figs. 1-2) (no. 2 in table 1) is very similar to the last, and only tapers less distinctly to the front. The talonid is two-thirds as high as the protoconid, and the cingulum at the anterior base is almost one-third as high as the main cusp. This specimen is of the right side; the groove delimiting the vertical ridge on the anterior slope of the protoconid on the lingual side is more clear-cut than that on the buccal side.

A third specimen, originating from Tjeleko, somewhat worn, has the posterior ridge and cusp as well developed as that in specimens 1 and 2

but is less wide posteriorly, though still wider behind than across the base of the main cone (pl. II fig. 10).

The largest P_4 in the Celebes collection from Sompoh, slightly worn, is broad (pl. II fig. 11), slightly more so behind than in front, and the anterior cingular point is largely cut out by the premolar in front of it. An almost equally massive P_4 is in situ in a right ramus of the mandible also holding M_2 (no. 5, pl. I fig. 7).

Several specimens of P_4, two of which are unworn, have an elliptical outline and are widest across the protoconid. Three examples are presented on pl. II figs. 3-8; these are specimens nos. 6-8 of table 1. As can be seen from the figures, the posterior ridge and cusp are not less well developed relative to the protoconid than those in the first mentioned specimens, being about two-thirds as high as the main cusp, but the cingulum does not form such a distinct transverse ridge behind, and consequently the crown is less extended transversely at the hinder end. The point formed by the anterior cingulum seen in the first described teeth is absent or only faintly developed in the teeth now under discussion.

Thus, the difference between the two types of P_4 is mainly one of degree of development of the cingulum in front and behind, a difference that cannot be accorded much weight in suid teeth, although it is being used in the classification of certain Siwalik forms. I regard the variation seen as of an individual nature only, and the P_4 of *Celebochoerus* thus can be defined as possessing a strong, uncleft, conical protoconid, a talonid that is only two-thirds as high, and a steep anterior slope of the protoconid without any elevation except, in most cases, a point rising from the base anteriorly that may reach one-third of the height of the protoconid at most. The width is greatest behind in specimens with a strong posterior cingulum that slopes outward and forward from the talonid cusp, and the width is greatest across the base of the protoconid in those specimens in which the cingula are less developed on either end of the crown.

Most of the P_4s in the Celebes collection are isolated specimens, but fortunately, in addition to the left P_3-M_3 (no. 1) there are four samples of a P_4 associated with a P_3 (pl. I figs. 4-6, pl. II fig. 9), showing that P_3 is slightly shorter and decidedly narrower than its P_4, and more slightly built. The protoconid of P_3 does not appear to be lower than that of its P_4 but, in keeping with the less width of the crown, the main cusp is not rounded but compressed transversely at the base. Except in its relatively less width P_3 differs from P_4 in the less development of the talonid cusp, which is only about one-half as high as the protoconid in a few unworn specimens, and in the anterior cingular point, if any, being smaller. The

roots of P_3 are two in number, of which the hind root is constricted or imperfectly divided in the median line and stronger than the anterior root.

In addition to the five P_3s associated with a P_4 we have three isolated specimens of P_3. Careful examination failed to disclose any sign of a contact facet on the anterior side of P_3, which indicates that in *Celebochoerus* P_2 does not develop. This is important as it shows the Celebes fossil suid to be more advanced in its premolar reduction than most of the recent or fossil species of Suidae with which we shall have to compare it on account of the similarity in shape of P_4.

Premolars of the type described above do occur in a number of fossil and living species of Suidae. The main basis of the classification of the Indian Suidae as given by Pilgrim in his 1926 monograph is the last lower premolar, P_4. Four main types can be distinguished, viz., 1) that in which the protoconid is cleft at the summit (*Dicoryphochoerus*), 2) that with a single main cusp (*Potamochoerus*), 3) that in which the front and back portions of the crown are so greatly elevated as to be almost as high as the protoconid (*Sus*), and 4) one-cusped but enlarged P_4s (*Conohyus, Sivachoerus, Tetraconodon*) (Pilgrim, 1926, p. 7/8). Pilgrim's emphasis on the P_4 has been criticized by Matthew (1929, p. 455), Pearson (1928, p. 69), and Colbert (1935a), all of whom agree that the chart given by Pilgrim is far too complex; Colbert's phylogeny, based on a revision of the whole material, shows the Suidae to be monophyletic through the early Tertiary, with their adaptive radiation beginning in the Oligocene, while Pilgrim assumed the Suidae to have been polyphyletic down to the base of the Tertiary. Colbert has further reduced the number of species, allowing more for individual variation than Pilgrim, but in essence Colbert's grouping of the various genera is much the same as that visualized by Pilgrim; although he combines groups 1-3 of Pilgrim (group IV, Colbert, 1935a, p. 5) each of the three forms a separate line.

It is with the *Potamochoerus* group that *Celebochoerus* has to be classified, for in this group we find P_4s which are nearest to those of the Celebes suid. Similarly shaped P_4s also occur in group 4 of Pilgrim but in *Celebochoerus*, as we shall see below, there is no evidence of the increase in size of P3 and P4 relative to the molars that characterizes this group. On the other hand, certain dental characters such as the shape of the lower male canine to be detailed further on make it evident that *Celebochoerus* does not quite agree with *Potamochoerus* and cannot be more than a closely allied form. It should be remembered that Pilgrim's work concerned the Indian Suidae exclusively, leaving out the Chinese and Malaysian forms with which we have to deal also. The babirusa has premolars which are

TABLE 1

Measurements of lower premolars of *Celebochoerus* [1])

No. of specimen	P_3 length	P_3 width	P_4 length	P_4 width
1	16.2	9.6	15.7	12.4
2			15.1	10.5
3			14.8	11.3
4			16.7	13.3
5			16.4	12.5
6			15.7	10.8
7			15.0	11.0
8			15.7	11.2
9	14.3	10.6	15.4	11.5
10	12.8	7.3	14.9	9.9
11	13.3	7.7	14.0	9.8
12	14.3	7.6	16.6	13.1
13			17.3	12.5
14			14.9	11.6
15			14.5	11.0
16			13.9	10.4
17			15.5	10.6
18	15.7	8.9	14.3	11.6
19	14.8	8.5	14.7	10.4
20	14.4	7.4	12.8	9.0

nearest to those of *Potamochoerus* (Stehlin, 1899, p. 170/171) but this form, again, is so aberrant in the development of its canines as to form a group of its own.

The lower premolars of *Potamochoerus palaeindicus* Pilgrim (1926, p. 27, pl. X fig. 2) and of *Potamochoerus theobaldi* Pilgrim (l.c., pl. X fig. 3), both presumably from the Pinjor zone, Upper Siwaliks, agree well in shape with those of *Celebochoerus* as above described but are much larger. The premolars of *Propotamochoerus hysudricus* (Stehlin) (Lydekker, 1884, p. 79, pl. VIII fig. 3; Pilgrim, 1926, p. 25, pl. X figs. 1a, 1b; see Colbert, 1935b, pp. 239-242) are only slightly larger than those from Celebes, but the Indian form, which originates from the Dhok Pathan zone, differs from *Celebochoerus* in the retention of the first and second premolars, and in the excess in length of P_3 over P_4. *Propotamochoerus ingens* Pilgrim (Lydekker, 1884, p. 84, pl. VIII figs. 4, 4a; Pilgrim 1926, p. 26) is, again, distinguished by its greater size from *P. hysudricus*, of which latter species Colbert (1935b, p. 242) assumes it to be a variant.

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1) In table 1 all specimens originate from Sompoh with the exception of nos. 3 and 16 which are from Tjeleko. The P_3 and P_4 recorded nos. 1, and 9-12 are associated specimens.

The closest approximation in size to our Celebes suid is found in *Propotamochoerus salinus* Pilgrim (1926, p. 23, pl. VII fig. 1) and *P. uliginosus* Pilgrim (l.c., p. 25, pl. VII figs. 2a, 2b) from the Chinji and Nagri zones. Colbert (1935b, p. 242) considers the two to be very likely synonymous. The lower premolars of *P. salinus* are elliptical in outline, and their front and back cingula are less developed than in the P_4 described as *P. uliginosus*, which is widest behind. It will be remembered that I found the same two types of P_4 among the Celebes material. However, in the Siwalik species there is a small secondary peak of the protoconid of P_4, which is not shown in *Celebochoerus*. The P_4 of the type ramus of *P. salinus* is more raised anteriorly than in any of the *Celebochoerus* P_4s in which the anterior slope of the protoconid is straight and more steep and in which the anterior cusp, if any, does not rise higher than one-third of the height of the main cusp. The posterior ridge and cusp of the Siwalik premolars are more elevated relative to the protoconid, too, as will be seen from a comparison of my figures 1, 3, 5, and 7 on pl. II with those given by Pilgrim (1926, pl. VII figs. 1a, 2a, and 3b). In all of these characters the Siwalik premolars agree closely with those of recent *Potamochoerus* (Stehlin, 1899, p. 147, describes the secondary inner cusp of P_4 in *Potamochoerus* as latent), and show an advance over the condition found in *Celebochoerus*. On the other hand, as I have already noted, in *Propotamochoerus* P_1 and P_2 are retained, while in *Celebochoerus* these premolars do not develop any more. In this respect *Celebochoerus* is more advanced even than *Potamochoerus* in which P_2 is still present in most of the cases.

Further fossil suid genera with one-cusped P_4 are distinguished by the enlargement of the premolars relative to the molars. In *Celebochoerus* (see pl. I figs. 1 and 7), as in *Potamochoerus*, P_4 is approximately as wide as M_1 and decidedly narrower than M_2, while in *Conohyus sindiensis* Lydekker (syn. *C. chinjiensis* Pilgrim, 1926, pl. II figs. 10a, 10b; Colbert, 1935b, p. 227) P_4 is decidedly wider than M_1 and approximately as wide as M_2, as in *Sivachoerus giganteus* (Falconer et Cautley) (Pilgrim, 1926, pl. IV fig. 1). In *Tetraconodon magnus* Falconer (Lydekker, 1876, pl. X) the lower premolars have so enormously developed that P_4 is one-half wider than M_2.

Among the living genera of Suidae only *Potamochoerus* and *Babyrousa* have lower premolars of the type found in *Celebochoerus*. P_4 in *Potamochoerus*, however, has the anterior and posterior cingula more elevated than those in the Celebes fossil suid, as in *Propotamochoerus*. Recently Thenius (1950) has created a new subgenus, *Postpotamochoerus*, for the inclusion of Schlosser's *Sus hyotherioides*, a type of pig from the Pliocene

of China and from the Pontian of Samos in which P_4 has a cleft protoconid in the *Sus* fashion and a much higher talonid and anterior and posterior cingula than has *Celebochoerus* (see Pearson, 1928, p. 59, pl. IV fig. 1, and Thenius, 1950, p. 29 fig. 2), and in which there are four premolars in the mandible against only two in *Celebochoerus*. The P_4 of *Babyrousa* is only smaller than that of *Celebochoerus*; a small postero-internal secondary cusp on the protoconid can sometimes be distinguished, of which there is no evidence in *Celebochoerus*. In its premolar reduction the babirusa has reached the same stage as *Celebochoerus*, there usually being only two premolars in each jaw. A P_2 was found only once among seventeen adult babirusa skulls from Buru, and twice among fifteen adult babirusa skulls from Celebes; only the race of the babirusa from the Sula islands has a higher incidence of second premolars, occurring in seven out of thirteen adult skulls (Hooijer, 1950a, p. 110).

UPPER PREMOLARS

The upper premolars of *Celebochoerus* are of interest as they conform well to the type of *Potamochoerus* and are as distinct from those of *Sus* as are the lower premolars of this Celebes suid.

P^3 and P^4 occur in situ in some maxillary fragments, three of the left and one of the right side (pl. VI fig. 3). The last-mentioned fragment also holds M^1 and part of M^2; one of the others has a broken P^3 but the full series of upper molars, well-preserved. In front of P^3 there is an alveolus, indicating the presence of a P^2. Thus, premolar reduction in *Celebochoerus* has not progressed as far in the upper jaw as in the lower, just like in *Potamochoerus* (Stehlin, 1899, p. 148).

There is one isolated right P^2 in the Sompoh collection, very similar to that in *Potamochoerus* both in shape and in size (pl. III fig. 12). This tooth, which measures 11.9 by 6.7 mm, has a contact facet posteriorly to the lingual side, and thus must have been placed obliquely in the maxilla, with the anterior end pointing forward and inward. P^2s rotated in the same way occur in several *Potamochoerus* skulls I have seen in which there is lack of space for the anterior premolars to erupt in the normal way because of the proximity of the canine.

DM^1 did not develop in *Celebochoerus*; a maxillary fragment from Tjeleko with the premolars broken off but holding the canine is sufficiently complete to show the absence of a tooth in front of P^2, of which latter in this specimen only the alveolus remains (pl. VI fig. 1).

P^3 can be described as a stout, sectorial tooth with an inner talon. It consists of a conical main cusp or paracone, and a well-developed cingular

ridge that forms the postero-internal corner of the crown. In unworn specimens this ridge is seen to overhang a narrow but deep pit or fossa that separates the cingular ridge from the paracone. This fossa is bounded anteriorly by the paracone, buccally by a ridge descending backward from the apex of the paracone, and behind and lingually by the cingulum, but it is open to the front internally as the cingulum is not, or hardly, developed along the inner surface of the paracone. The cingulum can again be traced anteriorly, where it forms a median point and in some cases envelops a tiny lingual anterior fossa as well.

The paracone is very broad at the base, forming a cone that occupies the whole width of the front part of the crown. This is a very marked difference from the P^3 in *Sus* in which the paracone is compressed transversely and in which the postero-internal fossa is wider, making the anterior portion of the crown less wide relative to the posterior part than in *Celebochoerus*. The *Sus* P^3 is further distinguished from that of *Celebochoerus* in the higher ridges descending backward and also forward from the apex of the paracone, and in the more strongly developed anterior cingulum that in *Sus* always encloses a distinct antero-internal fossa and occasionally even develops an anterior talon cusp (protocone) (Stehlin, 1899, p. 144).

The *Celebochoerus* P^3 differs from that of *Sus* in the same points as does that of *Potamochoerus*. P^3 in the latter genus resembles that of the Celebes suid closely, especially in its rounded instead of compressed paracone. The few unworn specimens available suggest that the ridges descending backward and forward from the apex of the paracone are somewhat better developed in *Potamochoerus* than in *Celebochoerus*.

The variation that can be observed in the nineteen complete specimens of P^3 of *Celebochoerus* (table 2, nos. 1-11 are of the right side, nos. 12-19 of the left; nos. 7, 9, and 18 are from Tjeleko, the remaining specimens are from Sompoh) is mainly that of size, and of development of the cingula. Four isolated specimens are represented on pl. III figs. 13, 18, 19, 20, 23, and 24. The posterior paracone ridge may bear a distinct but small cusp, the metacone, while in one of the figured specimens there is a well-defined cusp in the postero-internal fossa surrounded by the cingulum, the metaconule (pl. III fig. 20).

The morphological type of P^3 just described occurs in the fossil species of the genera *Propotamochoerus* (*P. salinus* and *P. uliginosus*, Pilgrim, 1926, pp. 24, 25, pl. VII figs. 4 and 7; *P. ingens*, l.c., p. 27, pl. VII fig. 8), *Potamochoerus* (*P. palaeindicus*, Colbert, 1935b, p. 243 fig. 111), and *Sivachoerus* (*S. giganteus*, Lydekker, 1884, p. 57, pl. XI fig. 2). Only the largest specimens in our series from Celebes (table 2) agree in size with those of

TABLE 2

Measurements of upper premolars of *Celebochoerus*

No. of	P^3		P^4	
specimen	length	width	length	width
1	12.0	10.5	13.0	15.3
2	17.4	13.4		
3	14.7	12.0		
4	13.5	10.2		
5	14.4	10.9		
6	15.0	12.5		
7	15.3	11.9		
8	16.3	12.6		
9	14.0	10.5	11.3	13.1
10	14.3	10.8		
11	13.3	9.9		
12	14.6	10.7	13.7	14.8
13	13.5	10.3		
14	14.8	11.0		
15	15.0	11.6		
16	15.8	12.9		
17	14.4	11.0		
18	14.5	10.9		
19	—	12.8		

Propotamochoerus salinus and *uliginosus*, and of *Potamochoerus palaeindicus*; the remaining Siwalik forms are decidedly larger.

As is the case in the mandible, there is no enlargement of the premolars relative to the molars in the upper jaw of *Celebochoerus*. In the Celebes suid, as in *Potamochoerus*, P^3 is decidedly less wide than M^1 (see pl. VI fig. 3). In *Sivachoerus* (Lydekker, 1884, p. 54, pl. XI fig. 2) P^3 is nearly as wide as M^1; in *Conohyus* the size relation of P^3 and M^1 is approximately the same (Pilgrim, 1926, p. 13, pl. II fig. 11), and in *Tetraconodon* (l.c., p. 16, pl. V) P^3 is very much wider than M^1.

The last upper premolar, P^4, is most abundant in the Celebes collection. We have five complete P^4s in situ in maxillary fragments (three of which associated with a P^3: nos. 1, 9, and 12 of table 2), and further sixty-nine isolated specimens, the measurements of which are given in table 3. Nos. 1-34 are of the right side, nos. 35-69 of the left. The variation in shape of P^4 is considerable (Stehlin, 1889, p. 143/144), and Pilgrim (1926, p. 7) considers it to be the least important premolar for classification purposes. However, there are fundamental differences between the P^4 in *Sus* and that in *Potamochoerus* (Stehlin, l.c., pp. 143 and 146). The two outer cusps, paracone and metacone, as well as the lingual cusp, protocone, are compressed transversely in *Sus*, making the central fossa very much wider than is

the case in *Potamochoerus,* in which the cusps are rounded. Furthermore, the anteroposterior ridge lingually of the paracone, free at the summit in *Sus,* is connected with the paracone up to its apex in *Potamochoerus.* In these characters the P^4 of *Celebochoerus* agrees with that of *Potamochoerus.*

With two exceptions to be noted below, all the Celebes fossil P^4s have a distinct cleft between paracone and metacone, traces of which remain

TABLE 3

Measurements of P^4 of *Celebochoerus* [1])

No. of specimen	length	width	No. of specimen	length	width
1	13.6	14.0	35	14.8	15.0
2	13.8	15.3	36	11.3	11.9
3	13.2	13.8	37	13.3	14.9
4	13.0	14.5	38	—	14.9
5	13.7	15.0	39	13.3	13.6
6	15.9	15.9	40	14.4	14.5
7	13.3	13.7	41	13.6	14.8
8	13.1	13.2	42	14.2	14.4
9	13.1	14.1	43	12.8	15.0
10	13.4	14.3	44	12.2	13.1
11	12.6	13.7	45	10.9	12.4
12	13.8	14.1	46	13.0	—
13	13.5	14.0	47	13.2	14.0
14	14.0	14.3	48	12.6	14.8
15	10.6	12.0	49	11.7	13.9
16	11.7	13.7	50	12.8	13.8
17	12.8	13.3	51	—	15.0
18	12.4	14.4	52	12.9	13.6
19	13.3	15.7	53	12.6	13.3
20	11.3	12.1	54	12.2	13.2
21	11.4	12.8	55	12.8	14.0
22	11.3	12.8	56	12.2	15.0
23	—	13.4	57	11.7	13.8
24	11.5	13.6	58	13.0	14.3
25	12.8	13.1	59	11.3	14.3
26	13.5	15.0	60	14.7	15.5
27	12.9	14.0	61	13.4	12.7
28	13.4	14.5	62	14.2	14.5
29	13.7	14.9	63	12.3	14.4
30	12.8	14.7	64	12.7	14.0
31	12.5	13.3	65	12.5	13.4
32	14.7	15.8	66	11.8	14.0
33	11.5	14.1	67	12.8	14.7
34	11.4	11.4	68	14.4	14.7
			69	12.8	14.3

1) In table 3, all specimens are from Sompoh except nos. 4, 14, 29, and 31, which have been obtained at Tjeleko.

visible even in the most worn specimens. In this character *Celebochoerus* agrees, again, with *Propotamochoerus* and *Potamochoerus* (Pilgrim, 1926, pp. 22 [1]), 24, pl. VII figs. 4, 5, 6, 8; Colbert, 1935b, p. 243 fig. 111). Some characteristic specimens (nos. 5, 13, and 40) are figured on pl. III figs. 14, 15, 17, and 22. In *Conohyus* (Pilgrim, 1926, pp. 12-14, pl. II figs. 3, 7, and 9) P^4 is characterized by its hypsodonty and "the feebleness of the cleft in the outer cusp"; P^4s of the same type occur in *Sivachoerus* (Lydekker, 1884, pl. XI fig. 2) and *Tetraconodon* (Pilgrim, 1926, p. 20, pl. III fig. 1b). Moreover, P^4 of these forms have an inner cingulum not shown in the Celebes specimens. Thus the *Conohyus-Sivachoerus-Tetraconodon* group distinctly differs from the *Potamochoerus* group, besides in having relatively larger premolars, in the cleft between the paracone and metacone of P^4 being feeble instead of distinct, as it is in *Celebochoerus* (see pl. III figs. 14 and 17).

In the long series of P^4s from Celebes there are two specimens, nos. 33 and 34, which are definitely anomalous (pl. III figs. 9 and 21). The metacone, which is always smaller than the paracone, appears to be so much reduced as to be practically absent, leaving only two cusps in nos. 33 and 34, the paracone buccally and the protocone lingually. In no. 33 the roots are partially preserved, and there are two of them on the buccal side, just like in normal specimens in which they support paracone and metacone respectively, and there is one internal root below the protocone, as usual. The reduction of the metacone as observed in these two specimens is an individual peculiarity that has no relation to the condition of P^4 in the *Conohyus* group in which the metacone is distinct but separated from the paracone only by a very slight cleft that is soon obliterated by wear.

LOWER CANINES

It is customary to distinguish between two types of (male) lower canines among the Suidae, the *scrofa* type and the *verrucosus* type. In the former the posterior surface is wider than the external, in the *verrucosus* type the posterior surface is narrower than the external, the internal surface being wider than either of these in both types. As the names imply, the first-mentioned type occurs in *Sus scrofa* L., and the second in *Sus verrucosus* Müller et Schlegel, from Java.

"The earlier species of *Sus* show a verrucose or sub-verrucose type of cross section in the lower canine of the male. This gradually becomes transformed into the scrofic type, but is retained in the modern species

1) Pilgrim (1926, p. 22, line 3 from bottom) writes "bicuspid character of the inner lobe"; this should read "outer lobe", cf., l.c., p. 24, line 6 from bottom.

Sus verrucosus and to a less extent in *Sus barbatus*" (Pilgrim, 1926, p. 59). The lower canine of *Potamochoerus* is midway between the two types, the posterior surface being either slightly narrower, or slightly wider than the external, and the same holds for fossil *Propotamochoerus* (Pilgrim, 1926, p. 23).

Celebochoerus (pl. I fig. 10) is markedly *verrucosus*-like in the cross section of its lower canine; I have eight fragments of lower canines from Sompoh and Tjeleko, and in all of these the posterior surface is narrower than the external. The measurements are given in table 4; nos. 1-3 are of the left side, nos. 4-8 of the right. All specimens originate from Sompoh except no. 4 which comes from Tjeleko. The measurements of no. 9 could

TABLE 4

Measurements of lower C of *Celebochoerus*

No. of specimen	1	2	3	4	5	6	7	8	9
internal	22.5	—	16.8	20.0	24.3	—	17.3	22.4	ca. 18
external	19.3	20.3	15.4	19.7	21.0	18.8	14.1	19.4	ca. 16
posterior	14.5	—	11.5	14.9	15.5	—	12.2	15.3	ca. 12

be given only approximately as this is a broken C in a fragment of a left mandibular ramus. The fossil specimens agree very well with those of recent *Sus verrucosus*: the posterior surface, the only surface that is not covered by enamel, has a median longitudinal groove, and two similar shallow longitudinal grooves are found on the external surface, one close to the anterior edge of the canine and the other in the posterior half of the surface. The internal surface, the widest of the three, is convex from edge to edge, most distinctly so in its posterior part. The enamel is faintly striated longitudinally; on the external surface a narrow strip of cement may be seen in some specimens.

Among the fossil Indian forms, the *verrucosus* type of lower C occurs in *Hippokyus, Dicoryphochoerus titan,* and *Sivachoerus giganteus* (Pilgrim, 1926, p. 6, pl. XX), which all differ from *Celebochoerus* in the structure or relative size of their premolars. Thus, the Celebes fossil suid presents the unusual combination of *Potamochoerus*-like premolars and *verrucosus*-like lower canines.

The babirusa, the lower canines of which differ from those of all other suids in being devoid of an enamel coating, has lower canines which present a *verrucosus* cross section, although both the internal and the external surfaces are convex. The shape of the cross section of the lower canine of the babirusa indicates that, if there are relations with the *Sus* phylum, these

must be with the *verrucosus*-group; this also follows from the considerations based on geography as the babirusa's habitat is within the geographic range of the *verrucosus* swine (Stehlin, 1899, p. 292). The same applies of course, to our new fossil suid from the Pleistocene of Celebes.

Sus celebensis, a member of the *verrucosus*-group (Nehring, 1889; Major, 1897), has male lower canines that agree with those of *Celebochoerus* but for their smaller average size. In a previous paper (Hooijer, 1950a, p. 107) I gave the measurements of seven recent and ten subfossil male lower canines of *Sus celebensis*; the ranges and means of these series can be compared with those of *Celebochoerus* in table 5.

TABLE 5

Variation ranges and means of dimensions of male lower canines of *Celebochoerus* and of *Sus celebensis*

	Celebochoerus		*Sus celebensis*			
			recent		subfossil	
	range	mean	range	mean	range	mean
internal	16.8-24.3	20.6	15.8-20.0	17.4	13.4-17.6	15.6
external	14.1-21.0	18.5	14.5-17.5	15.9	12.5-17.4	14.7
posterior	11.5-15.5	14.0	10.4-14.5	12.0	9.2-13.7	11.4

It is clear that the *Celebochoerus* canines exceed in average size those of the living *Sus celebensis,* while the *Sus celebensis* from caves and rock-shelters of Southwestern Celebes is again smaller, not only in its male lower canine but in all the teeth (Hooijer, 1950a, pp. 96-117). This was one of the few exceptions I know to the rule that subfossil or fossil remains of living species average larger than the corresponding recent (Hooijer, l.c., p. 147). *Celebochoerus,* however, has no close relationship to *Sus celebensis* because of its *Potamochoerus*-like premolars; this character removes it definitely from the ancestral line of the living *Sus celebensis.* Nor do the relationships between *Celebochoerus* and the babirusa appear to be close, for, although the babirusa has *Potamochoerus*-like premolars, there is no resemblance whatsoever between the highly aberrant upper canines of the babirusa and those of *Celebochoerus.*

UPPER CANINES

The upper canine of *Celebochoerus heekereni* was originally described by me (Hooijer, 1948a) as being subtriangular in cross section, slightly constricted at the pulp cavity, and with the anterior surface at right angles to the upper. The curvature of the canines is like in *Sus,* with the upper

surface at the inner curve and with a median longitudinal groove. From the transversely concave wear facet on the anterior surface it was inferred that the lower canines were small relative to the upper. While this was all confirmed by the material subsequently discovered and described for the first time in the present contribution, the statement made in the first description that the upper and anterior surfaces of the upper canine are coated with enamel proved to be mistaken; as I already remarked before (Hooijer, 1950b) the thick whitish layer on the holotype and the paratype is the weathered outer layer of the dentine, or a cement investment. If there is an enamel band on the canine, this is on the lower surface, as in *Sus* or in *Potamochoerus,* and the width of this strip of enamel is very variable. No enamel ridges are to be found on the upper anterior and posterior edges of the *Celebochoerus* canine; in this respect the Celebes canines differ from those of *Sus* or of *Potamochoerus* in which these ridges do occur. The ventral enamel band on the upper canine of *Celebochoerus,* if present, never shows the heavy longitudinal grooves shown in the ordinary suids but is perfectly smooth. It is evident that the enamel formation on the upper canine of the Celebes suid is much weaker than that in *Sus* and *Potamochoerus.*

I have now before me some one hundred and sixty specimens of upper canines. Unless otherwise stated these canines originate from Sompoh; a small number are from Beru or Tjeleko. Only very few are as complete as the right upper C figured previously (Hooijer, 1950b, pl. XVI fig. 2); most of the specimens are broken on both ends, or show either the pulp cavity or the tip of the canine. The preserved portions vary from 3 to 11 cm in length.

The largest upper C in the collection, of the right side (no. 1 in table 6, pl. V fig. 2) is a basal fragment only 6 cm long, showing the apex of the pulp cavity. In cross section it is similar to those already described (Hooijer, 1948a, figs. 1a, 1b, 1950b), subtriangular with rounded angles, the anterior surface at right angles to the upper and slightly narrower than the latter. The longitudinal grooves in the anterior and posterior surfaces are sharply pinched in. In this canine there is no ventral strip of enamel. The horizontal diameter is 43 mm, the vertical 39 mm.

The proximal part of a left upper C (no. 2, pl. VI fig. 4), $8^1/_2$ cm long, differs from the last in being more dorsoventrally compressed; the horizontal diameter is 44 mm, the vertical 38 mm. Each of the three surfaces has a shallow longitudinal groove. There is no enamel on this specimen either.

A much corroded specimen of a left upper C (no. 3) measures 42 mm horizontally and 36 mm vertically at the base, and agrees with the last

except in that it has a strip of enamel on the lower surface anteriorly, 10 mm wide at most.

Unfortunately none of these truly gigantic upper canines is complete. An almost equally large right upper C previously figured (Hooijer, 1950b, pl. XVI fig. 3), measuring ca. 42 by ca. 39 mm near the base, narrows only to 35 by 33 mm over a distance of 6 cm, thereby curving gently upward and somewhat backward. It is a safe guess that these canines have been at least 20 cm long in a straight line from base to tip. As seen in the practically complete right upper C already figured (Hooijer, 1950b, pl. XVI fig. 2) the wear facet made on the anterior surface by the lower canine begins to appear 5 cm from the base of the upper canine and does not extend quite to the tip; consequently the tips of the upper canines are clear of the lower ones. This is a condition that we find in the African genus *Phacochoerus*.

In the proximal fragments above described the anterior wear facet does not show yet. Four good portions of upper canines, two of the right and two of the left side (nos. 4-7, of which no. 5 is from Beru), vary form 9 to 11 cm in length, remain of much the same width and height throughout, but show a slight constriction at the pulp cavity and a gradual upward curve. The wear facet on the anterior surface appears some 4 to 5 cm from the base and is transversely concave as it is in the paratype upper canine of *Celebochoerus* (Hooijer 1948a, pl. I fig. 6) as well as in the almost complete specimen figured some years ago (Hooijer, 1950b, pl. XVI fig. 2). The tips of these four specimens are missing (pl. IV figs. 3-6). The anterior surface varies from 27 to 32 mm in width (table 6), and thus is much wider than the lower canine, the posterior surface of which is from 11.5 to 15.5 mm wide (table 4). In the fact that the lower canines are decidedly narrower than the upper, *Celebochoerus*, again, agrees with *Phacochoerus*, which shows similar concave wear facets on its upper C (Hooijer, 1948a, p. 1028). The wear facet in its full extent is seen in a large fragment of a left upper C on pl. I fig. 11; it does not extend to the tip, proving, once more, that in *Celebochoerus* the upper canine projects beyond the end of the lower.

There is some variation in the upper canines mentioned above: in no. 7 we notice the surface to be somewhat more distinctly grooved, especially proximally, than that in the other specimens. Of the three longitudinal grooves, one in each of the surfaces, noticed in the first description of the *Celebochoerus* canines (Hooijer, 1948a), the upper shows best in nos. 4 and 7, the anterior is well marked in all the specimens, but that in the posterior surface, again, is only faintly developed in nos. 5 and 6. In the last-

mentioned canines the posterior surface is more produced at the posterior lower edge of the canine than in the others, and the cross section therefore is subquadrangular rather than subtriangular. In none of these canines there is any trace of an enamel strip, the dentine being covered by cement all over.

Remain forty-five proximal fragments of upper canines (nos. 8-52 in table 6; nos. 8-26 of the right side, nos. 27-52 of the left) the greatest horizontal and vertical diameters of which can be given. Of these specimens, twenty [1]), or just under one-half of the total, have a ventral enamel band, situated anteriorly, so as to reinforce the anterior lower edge of the canine. It clearly limits the anterior wear facet below, preventing the extension of wear upon the lower surface of the upper canine. No enamel ridges occur along the upper anterior and posterior edges of the tooth, and these edges are, therefore, more rounded off, as in *Phacochoerus* canines which do not have enamel reinforcements along the edges either. The enamel usually is only 7 to 10 mm wide, and forms a longitudinal strip, smooth, or slightly striated but never grooved. In a few specimens the enamel strip is seen to peter out proximally (nos. 24, 29, and 31). In two specimens (nos. 27 and 42) the enamel band is 20 mm wide.

Twenty-three specimens of upper canines are rather narrow at the base, remaining very much so along their entire length. Their measurements will be found under nos. 53-75 in table 6; nos. 53-64 are of the right side, nos. 65-75 of the left. Already in my first paper on the *Celebochoerus* canines I have raised the question whether there would be a sexual difference in size of the canines (Hooijer, 1948a, p. 1030), and I now believe that this is the case indeed. The canines numbered 1-52 I take to represent males, and nos. 53-75 females. The female canine thus differs from the male only in its more slender build, and sexual difference in canine size is considerably less well marked in *Celebochoerus* than it is in *Sus*. In *Potamochoerus* there is hardly any difference between the canines of the two sexes (Stehlin, 1899, pp. 255-256), and the same holds for *Phacochoerus* (Stehlin, l.c., p. 279).

Of the twenty-three presumably female upper canines only seven (nos. 53, 57, 62, 64, 68, 70, and 75) display a ventral strip of enamel, less than one-third of the total number. The enamel varies from 1 to 13 mm in width. In one specimen, no. 53, the enamel strip which, as usual, borders the wear facet below and strengthens the anterior lower edge of the canine, narrows toward the base (pl. V fig. 5). Two left upper canines, nos. 65 and 66, are

1) Nos. 10, 16-18, 20-22, 24, 27, 29, 31, 33, 35, 37, 38, 42, 44, 46, 47, and 49.

almost complete from base to tip, very slender, and gradually curved upward, with wear facets extending from about 5 cm from the base to a few cm below the tip which remains entire (pl. V fig. 4); no. 65 measures $13\frac{1}{2}$ cm, no. 66 15 cm in a straight line from base to tip. The females of *Celebochoerus* likewise had upper canines the tips of which remained clear of the lower canines. The variation ranges and means of the dimensions of what I think are the male and the female upper canines of *Celebochoerus* are presented in table 7.

One canine, which I believe to be female, is in situ in a fragment of a left maxillary from Tjeleko (pl. VI figs. 1-2). This canine measures 24 mm horizontally and 21 mm vertically and has an 8 mm wide strip at the antero-inferior edge. Unfortunately the canine is broken off some 5 cm from the base, which is exposed on the upper surface of the fragment as the surface

TABLE 6

Measurements of upper canines of *Celebochoerus*

No.	1	2	3	4	5	6	7	8	9	10
horizontal	43	44	42	38	30	33	30	41	38	35
vertical	39	38	36	32	27	31	27	34	31	31
No.	11	12	13	14	15	16	17	18	19	20
horizontal	36	40	33	34	ca. 35	30	37	36	32	33
vertical	35	36	—	28	—	29	32	30	—	27
No.	21	22	23	24	25	26	27	28	29	30
horizontal	—	30	—	29	33	30	—	37	35	32
vertical	27	—	27	—	29	29	37	35	35	28
No.	31	32	33	34	35	36	37	38	39	40
horizontal	36	31	—	32	—	32	37	36	29	—
vertical	34	30	31	—	29	28	31	29	25	31
No.	41	42	43	44	45	46	47	48	49	50
horizontal	—	—	—	—	27	34	—	31	30	29
vertical	28	33	29	29	27	25	33	29	25	28
No.	51	52	53	54	55	56	57	58	59	60
horizontal	32	—	25	24	25	—	24	22	25	23
vertical	29	29	23	21	21	22	22	21	23	23
No.	61	62	63	64	65	66	67	68	69	70
horizontal	23	25	25	25	27	26	25	28	24	25
vertical	22	21	23	24	23	23	23	26	20	26
No.	71	72	73	74	75					
horizontal	27	—	27	25	25					
vertical	24	19	25	24	22					

of the maxillary laterally and above the base of the canine is lost. However, this specimen is important as it shows the true position of the canine relative to the premolars and the infraorbital foramen, and the way in which it is attached to the maxillary. The canine is so placed that it points outward and forward at its base, the line of the tooth making an angle with the anteroposterior line of the skull of about 60°, so that the bases of the right and the left upper canine, when seen in palatal aspect, diverge to the front at an angle of 120°, as they do in *Sus* or *Potamochoerus*. The canine has a gradual upward and backward curve; it is directed less forward but more

TABLE 7

Variation ranges and means of dimensions of male and of female upper canines of *Celebochoerus*

	male		female	
	range	mean	range	mean
horizontal	27-44	34	22-28	25
vertical	25-39	30	19-26	23

sideways than the canine in *Sus*, to the effect that it remains free of the lower canine at the tip, as we have already seen. In *Sus* or *Potamochoerus* the lower and the upper canine meet each other at a sharper angle and no part of the upper canine clears the lower one. In addition, there are other specific characters to be seen in this fossil fragment. There is a sheath of bone surrounding the base of the canine, forming a bony tube at least 5 mm in thickness and projecting outward and forward 4 cm beyond the vertical lateral surface of the maxillary above the premolars; this well-developed alveolus is clearly correlated with the relatively large canine, much larger, relatively as well as absolutely, than either in *Sus* or in *Potamochoerus*. Further, there is only a slight swelling of the bone above the canine alveolus, nothing like the crest (jugum caninum) that is so conspicuous in the boars of *Sus*, and even more so of *Potamochoerus* in which it forms a high anteroposterior bony ridge. In the absence of juga canina *Celebochoerus*, again, agrees very well with *Phacochoerus* which has a similarly strong tubular alveolus to accommodate the heavy upper canine, and no longitudinal bone ridge on it but just a slight swelling, in males as well as in females.

It is, perhaps, not superfluous, after having noted these very close resemblances in the canine region between *Celebochoerus* and *Phacochoerus*, viz., the heavy upper canines, much wider than the lower, that are abraded thus that the tips remain entire, the curvation of the upper canines more sideways than in *Sus*, and the development of a strong tubular alveolus for

the upper canine without any prominent longitudinal crest above, to repeat that the upper canine of *Phacochoerus* is very different from that of *Celebochoerus* in the way in which it is curved and the shape of its cross section (Hooijer, 1948a, p. 1028, fig. 1a-c). In the African genus the anterior upper and posterior lower surfaces are the widest, and the narrow posterior surface is situated at the inner curve instead of the broad upper surface. The *Phacochoerus* upper canine is distinctly curved backward, that of *Sus* curved upward, and in this respect *Celebochoerus* agrees with *Sus* rather than with *Phacochoerus*; the backward curvation in *Celebochoerus* is only very slight.

The upper canines of *Hylochoerus* (Thomas, 1905) resemble those of *Celebochoerus*; they are thick and heavy basally, and are wider than the lower ones. Although they even project a little beyond the ends of the lower canines, as in *Phacochoerus* and *Celebochoerus,* they taper more rapidly toward the tip, and there are juga canina above their alveoli which, however, are not as prominent as in *Sus* or *Potamochoerus.*

The alveolus for the upper canine in *Celebochoerus* is placed more backward relative to the premolars than in *Sus* or *Potamochoerus*; just beside the middle of P^3 the lateral surface of the maxillary abruptly curves outward to form the sheath around the canine; in the ordinary suids the maxillary expands only at the level of P^2. The large infraorbital foramen, however, is situated above P^4, as in *Sus* or *Potamochoerus.*

The premolars in the fossil fragment from Tjeleko are all broken off at the level of the palate; behind, the fragment shows the posterior outer and inner roots of P^4 which are entirely exposed on the fractured surface. The basal outline of the crown of P^3 can be seen, and P^2 is shown by the two alveoli for its anterior and posterior roots. The medial border of the fragment is the median maxillary suture. Anteriorly the fragment is broken off just in front of the canine alveolus. A few details on the palate of this fossil fragment can be given; these features, again, seem to be correlated with the heavy canines. Thus, the premolar rows diverge somewhat more distinctly outward to the front than in *Sus* or *Potamochoerus*; the distance of the inner border of P^4 to the median line of the palate is 13 mm, that from P^2 to this line, 20 mm. The width of the palate between P^4 is 26 mm, and that between P^2 is 40 mm. In ordinary suids the difference between these two palate widths is less. In *Phacochoerus* the anterior premolars do not develop, but the ridges on the palate in front of P^3 diverge as distinctly as do the premolar rows in *Celebochoerus.* Further, the palatine groove in the fossil fragment is not approximately straight as in *Sus* or *Potamochoerus* but is curved in its course: from back to front it first follows

the line of the premolars, just internally of the canine it is at its greatest distance from the median line, and then it smoothly curves inward again. We find exactly the same course of the palatine grooves in *Phacochoerus* and *Hylochoerus,* in which the grooves are farthest apart between the canine bases.

The distance of the outer surface of the fossil maxillary at the base of the infraorbital foramen above P^4 to the median line of the skull is 28 mm, making for a width of the palate across the lateral alveolar margins of the maxillary at P^4 of 56 mm. This, as well as the palate width between P^4 (26 mm), points to a palate of the same width as that in *Potamochoerus* or *Phacochoerus*; in *Sus scrofa,* especially in boars, the palate is decidedly wider.

There only remains to be discussed the tip of the upper canine, which is broken off in most of the specimens already dealt with above. I have over eighty, mostly small, fragments of canines in which the tip is more or less nearly entire, but of these specimens no measurements can be given. Some good fragments are presented on pl. I fig. 9, and pl. V fig. 1. Two, both of the right side (pl. IV figs. 1-2) are of great interest as they show a small cap of enamel, from which three ridges continue along the sides of the tooth, one along the anterior upper edge, one along the posterior upper edge, and one along the lower surface anteriorly. Both of the upper enamel ridges peter out at about 2 cm from the tip; the lower enamel strip, stronger developed than the others, continues to the broken edge of the fragment. It is quite certain that in the two upper enamel ridges at the tip of the *Celebochoerus* canine we find the homologues of the enamel ridges on the anterior and posterior upper edges of the upper canine in *Sus* or *Potamochoerus*. Of the three ridges that are seen to run out from the enamel capping of the tip only the lower continues along the surface of the canine toward the base, and could be observed in about one-half of the male upper canines, and in about one-third of the female upper canines of *Celebochoerus,* in which no trace of upper enamel ridges were found. Stehlin (1899, p. 278, fig. VI) has dealt at length with the homologies of the surfaces of the *Phacochoerus* upper canine to those of *Sus,* basing himself on the characters of the enamel capping he found on unworn tips of *Phacochoerus* canines (see Hooijer, 1948a, p. 1028). It is now clear that, in the case of *Celebochoerus,* as already surmised (Hooijer, l.c., p. 1029) the upper surface at the inner side of the curve is homologous to that in *Sus*; the two canines are curved in the same way, upward rather than backward (as in *Phacochoerus*). The *Celebochoerus* upper canine is, in a way, intermediate between that of *Sus* and of *Phacochoerus* since it has preserved, in a number

of cases, the ventral enamel band; in *Phacochoerus* even this last of the three enamel ridges that occur in *Sus* has got lost.

Among the fossil Suidae, none agrees with *Celebochoerus* in the peculiar shape of the cross section and in the restriction of the enamel to one band anteriorly on the lower surface of the upper canine.

I have indicated a sexual difference in size in the upper canines, referring 52 specimens to males and 23 to females. Whether or not there is a similar sexual difference in size in the lower canines I do not venture to decide. It seems probable, however, that, in table 4 above, nos. 3, 7, and, perhaps, 9, belong to females, being smaller than the remaining six specimens. If this is true, the female canines are about three-fourths as large in linear dimensions as the male canines and this is exactly the same ratio that I found for the upper canines. There is no difference in the shape of the cross section between the large and the small lower canines, and this was to be expected as the female lower canine, even in species in which the male lower canine is *scrofa*-like, remains *verrucosus*-like in cross section.

LOWER INCISORS

A small number of lower incisors in the Sompoh collection offer some points of interest. On the whole they resemble those of *Sus* or *Potamochoerus*. I_1 has a median longitudinal ridge on the lingual surface, thickening toward the root, and is laterally compressed. The lateral and the medial surfaces of the crown narrow toward the cutting edge, and are marked off from the convex labial surface by distinct but rounded edges. I_2 is larger than I_1, and asymmetrical; the groove limiting the median lingual ridge laterally is much deeper than that in I_1 and is displaced outward. The crown of I_2 is expanded laterally and the lateral surface passes smoothly into the labial (Stehlin, 1899, p. 309). The compression of I_2 is not transverse but oblique, above and medially—below and laterally. However, while in *Sus* the crown enamel extends much further rootward on the labial surface than on the lingual, in *Celebochoerus* the enamel extends rootward only very slightly more labially than lingually. I have several specimens of I_1 and I_2, two of which, of the left side, are from one and the same individual as their contact facets match each other precisely. They are figured on pl. III figs. 1 and 4. These teeth are only slightly worn along their transverse edges (in I_2 wear has also begun on the median lingual ridge), and, while the crown width of I_1 is 10.5 mm, and that of I_2 11.4 mm, in both teeth the height of the crown from the cutting edge to the base of the enamel is only 18 mm labially, not even twice the transverse width of the crown. Lingually, the enamel is broken off to a slight extent at the base, but as far as pre-

served the enamel height is 14 mm in I_1 and 16 mm in I_2, almost as much as the labial height. In an isolated right I_1, again very slightly worn only, the crown width of which is 8.7 mm, the gingival border of the enamel is 17.8 mm from the cutting edge labially and 15 mm lingually (pl. III figs. 2-3).

Checking at random a number of recent and fossil unworn or slightly worn lower incisors of *Sus*, I found the enamel to extend much further rootward on the labial surface than on the lingual. The enamel on the labial surface of lower incisors in *Sus* is three to four times as high from edge to gingival border as the crown is wide, against only two times in *Celebochoerus*.

It is quite clear that the lower incisors of *Celebochoerus* are decidedly less hypsodont than those of *Sus*.

The root of the fossil I_2 (that of I_1 is broken off) is seen to taper toward the tip; in this respect the *Celebochoerus* lower incisors also are less hypsodont than those of *Sus*. The *Potamochoerus* lower incisors are as specialized as those of *Sus*. The primitive traits in the lower incisor dentition of *Potamochoerus* as compared to *Sus* mentioned by Stehlin (1899, p. 316) only concern their more heavy build and relatively stronger I_3. I have not been able to recognize an I_3 among the small number of fossil fragments, but the I_1 and I_2 of *Celebochoerus* are more heavily built than those of any living species of *Sus*. An isolated right I_2 from Sompoh even measures 13 mm transversely. Incisors of that size occur in *Sivachoerus giganteus* (Falconer and Cautley, 1847, pl. 71 fig. 18), and exceed even those of *Dicoryphochoerus titan* (Lydekker, 1884, pl. IX). No close comparison needs to be made with the lower incisors of *Babyrousa*, fully hypsodont and almost completely barren of enamel, or with the degenerate lower incisors of *Phacochoerus*. The lower incisors of *Hylochoerus* (Bouet and Neuville, 1929, figs. 5-7, 35, 36, 39, and 40) are as reduced as those of *Phacochoerus* (Bouet and Neuville, l.c., fig. 45) and moreover the *Hylochoerus* I_2 has a cusplet on its lateral edge not shown in *Celebochoerus*.

UPPER INCISORS

Fourteen isolated specimens of I^1 from Sompoh and Tjeleko, ten of the right side and four of the left, differ from that in *Sus* in the same point as do the lower incisors: the upper central incisor is less hypsodont in *Celebochoerus* than it is in *Sus*. Added to that they are larger, and more distinctly recurved inward at the apex of the crown medially. I figure one right and one left specimen in posterior lower aspect (nos. 10 and 11 of table 8) to show the variation in development of the inner cingulum, a continuous ridge in the first, and an interrupted ridge in the second specimen (pl. III figs. 7 and 10). No. 11, the only specimen from Tjeleko, is the

largest I^1 in the collection. In all unworn or slightly worn I^1s of *Celebochoerus* the height of the enamel on the labial surface is one-half higher than the crown is wide (pl. III figs. 5 and 8), the width being that of the labial surface, while in *Sus* the enamel height on the labial surface of I^1 is at least two times the width of the labial surface. Furthermore, *Sus* I^1s are not curved inward at the apex of the crown to the extent shown in *Celebochoerus*. The small contact facets on the apex medially are as in *Sus*, proving that the right and the left central upper Is made a contact in the median line, as in that genus.

TABLE 8

Measurements of upper incisors of *Celebochoerus*

No.	1	2	3	4	5	6	7	8	9
width of labial surface	14.6	15.4	14.7	14.4	15.8	13.2	15.5	18.2	15.4
labiolingual diam.	8.7	8.5	7.9	7.6	8.8	7.6	9.0	9.6	8.5
No.	10	11	12	13	14				
width of labial surface	14.5	19.4	—	13.1	—				
labiolingual diam.	7.9	10.3	8.2	7.7	7.4				

There is not a single I^2 or I^3 in the collection from Celebes. Of course this does not mean that these elements did not develop in the *Celebochoerus* dentition. I^1 is a well-developed tooth, far from degenerate as it is, e.g., in *Phacochoerus* or *Hylochoerus* in which I^2 and I^3 are absent. In all probability *Celebochoerus* possessed at least one lateral upper incisor, for the evidence of which we have to await further material.

LOWER MOLARS

Molars are generally considered to be of little use for purposes of suid classification. In certain recent and fossil suids that can readily be distinguished by the characters of their canines or their premolars, the molars are deceivingly similar. Thus, the molars do not permit of a distinction between the *Sus verrucosus* group and the *Sus scrofa* group (Stehlin, 1899, p. 70). On the other hand, no consistent differences can be noticed between the molars of *Potamochoerus, Propotamochoerus, Dicoryphochoerus, Sivachoerus,* and *Tetraconodon* (Pilgrim, 1926, pp. 22-23).

However, the study of the molars is not as unpromising as this may sound, for it is possible to distinguish between the molars of *Sus* and those

of *Potamochoerus,* although these differ in degree rather than in kind. The molars of *Sus* are more complicated than those of *Potamochoerus.*

Each of the main cusps in a *Sus* molar has deep radial folds in the anterior, median, and posterior surfaces that lead to the formation of little enamel lobes upon wear, as in the molars of advanced hippopotami. The lobes of the cusps often can be seen to project into the transverse valley. Because of this, and, further, because of the presence of accessory conules at the entrances to the valleys and the transversely extended central cusps, the valleys in a *Sus* molar are rather narrow clefts. In *Potamochoerus* the enamel of the cusps of the molars is thicker than that in *Sus,* and it lacks the extensive radial folding. The enamel folds are weaker, and the lobes smaller than in *Sus.* There also are fewer accessory conules in the valleys, and the central cusps are less extended transversely. Consequently, the valleys between the cusps are wider, more open, than those in *Sus.* The main cusps in a *Potamochoerus* molar are, so to say, more individualized than those in *Sus.*

The molars of *Celebochoerus* possess the comparatively simple structure seen in *Potamochoerus* as well as in many fossil suids. There is, of course, an amount of variation, and this is well illustrated by the left lower molar series from Sompoh already figured on pl. I figs. 1-2, and the complete right lower molar series presented on pl. I fig. 3. The thickness of the enamel is displayed in the right M_2 shown in the mandibular ramus also holding P_4 of pl. I fig. 7. Firstly, the molars are comparatively wider in the left lower molar series than in that of the right side. Further, the left molars have a distinct tubercle at the lingual entrance to the transverse valley, most strongly developed in M_2, while at the buccal entrance to the valley there is an array of small conules obstructing the valley. In the right molar series there is no excess enamel formation at all; the cusps are perfectly simple, with very weak folds and wide valleys in between, open down to the bottom. The talonid of M_3, separated from the posterior pair of cusps by a transversely folded portion of enamel, is semicircular in outline, and consists of a larger outer and smaller inner portion. It conforms well with the description of the talonid of M_3 in *Potamochoerus* as given by Stehlin (1899, p. 71). Actually, the talonid of M_3 as seen in the series of *Potamochoerus* skulls in the Leiden Museum, although most often subdivided by an anteroposterior cleft into a larger buccal and a smaller lingual cusp, may also bear two cusps of much the same size, flanked by small basal ones, or the inner talonid cusp may exceed the outer somewhat in size. A similar amount of variation is observed in *Celebochoerus*; there is, indeed, a striking resemblance between the two genera in this point.

Besides the left and right lower molar series already discussed above, the measurements of which will be found under nos. 1 and 2 in table 9, there is a complete left lower molar series (no. 3 in table 9), two right M_{2-3}, associated (nos. 4 and 5), and further mostly isolated specimens. In table 9, nos. 6-20 are of the right side, nos. 21-29 of the left. All specimens originate from Sompoh except no. 24 of M_2 and of M_3 which are from Beru, and nos. 7, 11, 21, and 25 of M_2, and nos. 12, and 25 of M_3, which are from Tjeleko. No. 6 of M_2 is the molar in situ in the right mandibular ramus with P_4 (no. 5 of table 1, pl. I fig. 7). There is not much to be said about M_1 or M_2; they vary between the extremes figured on pl. I fig. 1, and pl. I fig. 3 (nos. 1 and 2). The lingual basal conule so conspicuously developed in M_2 no. 1 is also present, although of smaller size, in nos. 15

TABLE 9

Measurements of lower molars of *Celebochoerus*

	M_1		M_2		M_3	
No. of specimen	length	width	length	width	length	width
1	15.7	13.2	19.8	16.3	30.7	17.6
2	16.4	11.6	19.7	13.9	29.6	14.9
3	17.4	11.5	21.0	15.0	31.4	16.8
4	—	—	—	15.5	30.6	16.9
5	—	—	20.0	14.4	29.6	15.8
6	18.1	12.8	21.3	16.4	34.6	17.2
7			25.0	17.8	30.8	16.1
8			22.7	14.0	31.5	16.6
9			22.4	15.3	27.4	15.8
10			24.2	16.9	32.5	17.7
11			21.5	14.4	29.0	15.4
12			21.3	15.0	30.2	15.0
13			20.2	13.7	31.3	15.4
14			20.5	14.5	28.0	14.6
15			20.7	15.4	28.7	15.0
16			21.2	14.5	29.0	14.7
17			22.3	14.4	26.7	14.7
18			20.0	14.7	26.0	12.8
19			21.8	13.4	32.2	16.3
20			22.3	15.9	30.0	16.2
21	18.7	11.9	20.7	13.7	31.8	17.0
22	19.2	12.6	21.0	14.5	29.1	15.3
23			22.8	15.8	25.8	15.5
24			19.8	13.6	27.4	15.5
25			20.8	15.3	32.8	17.5
26			23.9	16.3	29.0	17.7
27			21.9	15.4	31.4	15.1
28			21.3	14.1	28.4	16.7
29			23.0	16.7	34.0	17.2

and 23 of M_2; in most specimens there are no accessory tubercles at the lingual entrances to the transverse valleys, which are very wide. The central cusp always forms a bridge between the anterior inner cusp (metaconid) and the posterior outer (hypoconid), and the lingual cusps are higher than the buccal, as is usual in the Suidae.

Variations in talonid development of M_3 can be seen on pl. II figs. 12-19. The isolated specimens figured, four of the right and four of the left side (nos. 6-9 and 21-24 of table 9) present different stages of wear, first at the buccal and then at the lingual cusps. The metaconid-hypoconid bridge is distinct, and on either side of this bridge the valleys are wide because of the absence of accessory conules and of any lobe-formation of the cusps; this distinguishes a *Celebochoerus* molar at once from a *Sus* molar. The talonid is very short in all of the specimens, horseshoe-shaped, with or without basal conules on the lingual side of the central cusp that connects the talonid with the posterior pair of cusps. The lingual part of the talonid is smaller than the buccal, and often forms two cusps behind one another. The talonid never attains the width of a pair of main cusps; in one specimen (no. 23, pl. II fig. 18) it is almost unicuspid. The anterior cingulum is weakly developed [1]).

The length and complication of the last lower molar varies much in recent and fossil pigs; in most of the recent suids (see Miller, 1906) the talonid of M_3 is longer than that in *Celebochoerus,* forming a transverse pair of cusps fully as large as the main cusps, and with a terminal heel that may consist of from one to nine cusplets (cf. *Sus barbatus oi* Miller (1906, pl. XLIX fig. 3) and *Sus cristatus* Wagner (Miller, l.c., pl. LIX figs. 1-2)).

Dicoryphochoerus titan (Lydekker, 1884, p. 61, pl. VII fig. 4; Pilgrim, 1926, p. 39, pl. XIII fig. 2), in spite of its somewhat more complicated molar structure, has the short M_3 talonid of *Celebochoerus heekereni* but is much larger; *Dicoryphochoerus vagus* Pilgrim (1926, p. 43, pl. XV figs. 1-2) is of the same size as the Celebes fossil suid. However, as its generic designation indicates, it has a bicuspid P_4.

Propotamochoerus hysudricus (Lydekker, 1884, p. 81, pl. VIII figs. 3, 3a) has a talonid as short as that of *Celebochoerus heekereni* but this talonid

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1) M_3 no. 24 (pl. II fig. 19) has a distinct anterior cingulum, much stronger than that in any other specimen I have seen. Usually, at the stage of wear attained by the specimen, there is an extensive concave wear facet on the anterior surface, and the cingulum is largely cut out by the M_2 (cf. nos. 8, 9, and 23, pl. II figs. 14, 15, and 18). In no. 24, however, interproximal pressure and wear appear to have been very weak between M_2 and M_3, for the anterior cingulum is very nearly intact.

is much lower than that in the Celebes fossil suid. The lower jaw figured by Pilgrim (1926, pl. X fig. 1a) as belonging to *P. hysudricus* shows the presence of P_1 and P_2 by which *Propotamochoerus* differs from *Celebochoerus*. Like *Dicoryphochoerus vagus, Propotamochoerus hysudricus* is of the same size as *Celebochoerus heekereni,* and so is *Sus adolescens* Pilgrim (1926, p. 60, pl. XX figs. 2a, 2b) which has a very short talonid for a *Sus* species, much like that of *Celebochoerus,* from which latter it differs, as a *Sus,* by its more complicated molar structure and the anteriorly and posteriorly elevated P_4.

The simple structure of the molars of *Celebochoerus* is retained in the babirusa which, moreover, has the same short talonid to M_3 that we found in *Celebochoerus* as well as, e.g., in *Propotamochoerus hysudricus* (Stehlin), *Dicoryphochoerus vagus* Pilgrim, and *Sus adolescens* Pilgrim. As Lydekker (1884, p. 49) wrote, in cases where only the last molars of some of the more generalized fossil forms are known it would be difficult to distinguish between these and the babirusa.

In 1948, along with two portions of very large upper canines, I received four last molars and an M^2 from Beru and Sompoh (Tjabengè) that were not very large and of a generalized suid structure. This was the first evidence of fossil suids in the island of Celebes. I did not, then, give serious consideration to the possibility that the canines and the molars belonged to the same species. The canines were unlike any upper canines known in recent or fossil suids at that time, and they evidently represented a new endemic genus and species of Suidae for Celebes. The molars, however, happened to resemble those of *Babyrousa* closely, the only difference that could be perceived being the somewhat larger size of the fossil specimens as compared with the recent. Fossil remains of living species generally are larger than corresponding recent material. Therefore, after having based my new genus and species *Celebochoerus heekereni* on the large upper canines (Hooijer, 1948a), I went on to describe the molars as *Babyrousa babyrussa beruensis* (Hooijer, 1948c).

If we now compare the series of last lower molars of pl. II figs. 12-19 with those ascribed to a fossil race of babirusa (Hooijer, 1948c, figs. 2 and 5) it will be observed that there is no difference; the 1948 M_3s from Beru and Sompoh are within the variation limits of those dealt with in the present paper. The molars are the least characteristic part of the dentition of the babirusa (Stehlin, 1899, p. 76). Furthermore, in the rich collection of fossil suid teeth now available there is not a single fragment of the highly characteristic canines of the babirusa that would enable us to establish the presence of babirusa beyond any doubt.

The evidence of the existence of *Babyrousa* in the Tjabengè fauna is not very convincing after all. If *Babyrousa* had been present in the fossil fauna beside *Celebochoerus* we should have expected to find at least some of its more characteristic teeth in the larger collection now at hand. On the other hand, the fact remains that the *Celebochoerus* molars, being of a generalized suid type, are indistinguishable from those of *Babyrousa* but for their larger size. If I had had only the molars of the fossil Celebes suid there would have been no obvious reason for not simply referring them to a fossil race of the babirusa. Now that we have large series of upper and lower canines, all without exception of the *Celebochoerus* type, the odds are against *Babyrousa* (or *Sus celebensis,* for that matter) being represented in the fossil fauna of Tjabengè. Therefore, I have placed *Babyrousa babyrussa beruensis* with a query in the synonymy of *Celebochoerus heekereni.* I feel, however, that we should not definitely rule out the possibility that babirusa did exist at the time of the *Archidiskodon-Celebochoerus* fauna; I shall return to this problem at the end of the present paper.

UPPER MOLARS

Molars of the upper jaw are more abundantly represented in the Celebes collection than the lower molars; there is one full series of left upper molars in a maxillary also holding P^{3-4}, one good right M^{1-3} (pl. V fig. 7), two left M^{2-3}, and many isolated upper molars. The measurements of the above mentioned specimens will be found under nos. 1-4 of table 10; of the following specimens, nos. 5-30 are of the right side, nos. 31-57 of the left. No. 5 of M^1 occurs in a right maxillary fragment with P^{3-4} (pl. VI fig. 3). All the specimens originate from Sompoh, with the exception of no. 8 of M^1, no 14 of M^2, and nos. 16 and 28 of M^3, which are from Tjeleko, and of no. 23 of M^2, which comes from Beru.

The left maxillary fragment with P^3-M^3 shows the expansion of the maxillary beside the middle of P^3, forming the alveolus for the large canine, which, as said above, is placed more backward in *Celebochoerus* than it is in *Sus* or *Potamochoerus.*

The upper molars of *Celebochoerus* have the same characters as the lower molars: the grooving of the cusps, so conspicuous in a *Sus* molar, is only very weak, and there are no lobes to the cusps or strong basal conules at the transverse valleys. The talon of M^3 is short, as it is in all species which also have a short M_3 talonid. It consists of one cusp, which may be as large as a main cusp basally but is less high, and which is placed inward, behind the metaconule, and buccally of which there may be a basal accessory conule. The cingulum, usually developed anteriorly only, in some specimens

continues around the antero-buccal corner of the crown, and can be traced again at the buccal entrance to the transverse valley and behind the metacone. Such an exceptional specimen (no. 9) is figured on pl. III fig. 6, beside two specimens of M^3 with very short talons (nos. 18 and 24). M^3 is much more variable in length than in width, and most of the variation in length is on the part of the talon (pl. III figs. 6, 11, and 16).

Upper molars of the same size, generalized structure, and simple M^3 talon occur, again, in *Propotamochoerus hysudricus* (Stehlin) (see Pilgrim, 1926, p. 26, pl. IX fig. 1). The babirusa also agrees with *Celebochoerus* in these latter respects, only the size of the molars is less. The M^2 and M^3 that I originally referred to babirusa (Hooijer, 1948c, figs. 3 and 4) are within the limits of the extensive series of these molars now available (table 10). As I said above in connexion with the description of the lower molars, it is more probable than not that babirusa did not actually form part of the Tjabengè fauna, for in the present large collection there is no conclusive evidence of the presence of *Babyrousa* such as would be afforded by portions of its characteristic canines.

In concluding the description of the dentition of the fossil suid from Celebes it might be said that there is reliable evidence only of one species of Suidae in the Tjabengè fauna, viz., *Celebochoerus heekereni* Hooijer. The earlier identification of babirusa from that fauna (Hooijer, 1948c) rests upon rather uncharacteristic specimens, and no decisive evidence of the occurrence of babirusa has been obtained since.

It will have been noticed from tables 9 and 10 that first molars are very scarce in the collection as compared with second or third molars. M^1 and M_1 are the first elements of the permanent dentition to erupt, and in individuals in their prime these molars are becoming much worn down, with little chance to have them preserved intact in fossil collections. The conclusion seems warranted that, in the Pleistocene of the Tjabengè area, *Celebochoerus heekereni* formed a thriving population.

TABLE 10

Measurements of upper molars of *Celebochoerus*

	M^1		M^2		M^3	
No. of specimen	length	width	length	width	length	width
1	16.4	15.2	20.3	17.9	29.7	18.4
2	15.5	14.5	19.4	16.4	25.8	18.3
3	—	—	20.5	17.4	28.0	19.3
4	—	—	22.0	17.1	28.8	18.8
5	19.0	15.1	21.4	18.1	26.8	18.5
6			21.6	17.1	27.7	18.4
7			22.0	18.2	29.7	20.0

No. of specimen	M^1		M^2		M^3	
	length	width	length	width	length	width
8			21.2	15.7	25.0	18.4
9			22.4	17.7	28.9	19.5
10			21.7	17.4	25.4	18.4
11			20.0	17.7	24.0	16.6
12			19.2	15.2	28.7	19.8
13			21.6	16.9	25.1	18.5
14			22.2	18.7	26.3	18.8
15			19.6	15.4	31.5	19.4
16			20.1	17.3	28.3	18.3
17			22.9	18.5	30.9	18.7
18			19.6	16.6	26.2	17.8
19			21.6	17.3	25.8	18.0
20			20.8	18.6	27.7	18.6
21			20.6	18.3	31.4	21.1
22			20.2	16.8	31.9	21.5
23			20.0	16.8	27.2	18.4
24					23.5	18.2
25					26.4	18.4
26					25.6	18.4
27					29.6	19.7
28					26.6	18.5
29					27.7	18.6
30					25.3	19.7
31	19.0	16.1	21.7	17.5	28.5	19.0
32	18.4	15.3	22.3	17.6	29.0	18.7
33	17.6	14.6	20.8	16.7	24.2	15.3
34			21.9	17.5	23.8	15.8
35			20.8	16.6	22.4	15.3
36			19.3	16.6	27.7	19.3
37			23.4	18.5	25.5	16.8
38			20.3	16.3	25.0	16.6
39			21.3	16.4	25.6	17.8
40			20.8	16.5	24.2	17.4
41			21.2	15.9	26.9	18.0
42			20.0	16.6	28.0	18.6
43			19.9	16.0	29.4	20.0
44			20.6	17.6	24.9	17.5
45			21.0	16.7	24.9	17.0
46			20.0	15.8	26.9	18.2
47			21.4	18.4	29.5	20.4
48			17.6	16.2	25.9	17.0
49	15.7	13.7	20.9	16.8	26.6	17.8
50					27.4	18.4
51					23.4	15.0
52					26.7	16.5
53					27.7	18.8
54					28.5	16.8
55					25.8	17.4
56					26.4	18.5
57					23.1	16.4

CRANIUM AND MANDIBLE

A large skull fragment from Sompoh shows some of the specific characters of *Celebochoerus heekereni*. Unfortunately the specimen is in a rather bad state of preservation. Anteriorly it is broken off just behind the infraorbital foramina, which, as we have seen (p. 21) are above P^4. Little is preserved of the dorsal surface of the skull, which is broken off behind the anterior zygomatic roots.

The posterior portion of the palate, with all the molars broken off but visible in outline, shows the two palatine foramina, the right one beside the middle of M^2 and the left placed beside the anterior border of M^3. There is a median ridge on the palate which flattens out behind. The palatines extend about 13 mm behind M^3 in the median line, and the pterygoid processes are missing. The palate width between M^3 is 26 mm.

On the right side the zygomatic process of the maxillary is preserved as well as most of the lacrimal and the anterior portion of the jugal. The facial crest that extends forward from the zygomatic process is entire. Further, the preorbital fossa is well shown, but the sutures between the lacrimal, the jugal, and the maxillary which concur in its formation cannot well be distinguished.

This very region of the skull is of systematic significance; in it we find some characters in which *Celebochoerus* differs markedly from *Sus* but agrees with other suid genera such as *Propotamochoerus, Phacochoerus,* or *Hylochoerus.*

The zygomatic process of the maxillary in the fossil skull shows a remarkable abruptness, much like that seen in *Potamochoerus* in contradistinction to *Sus.* In *Potamochoerus,* when seen from above, the facial crest that emerges a few cm behind the infraorbital foramen and that runs backward and out into the lateral eminence of the jugal, forms an angle with the anteroposterior line of the skull of about 110°. It is much more nearly perpendicular to the surface of the cheek than the facial crest in *Sus,* which forms an angle of about 135° with the anteroposterior line of the skull. In *Celebochoerus,* the zygomatic arch springs out almost as abruptly as in *Potamochoerus,* the angle between the facial crest and the anteroposterior line being 115°.

In *Sus* as well as in *Potamochoerus* the zygomatic process of the maxillary is placed above M^3; a line drawn vertically upward between M^2 and M^3 passes entirely in front of the jugal. In *Celebochoerus,* however, the point of contact between M^2 and M^3 is just below the middle of the zygomatic process of the maxillary, and the whole of the facial crest is anterior

to it. The anterior border of the orbit is above the posterior border of M^3 in *Sus* and *Potamochoerus,* while it is above the middle of M^3 in *Celebochoerus.*

Thus, the anterior zygomatic root and the orbit are placed more forward relative to the molars in *Celebochoerus* than they are in *Sus* or in *Potamochoerus.*

The genus *Propotamochoerus,* from the Lower and Middle Siwaliks (Chinji, Nagri, and Dhok Pathan zones: Colbert, 1935b, p. 34) differs even more strongly in these respects from the recent forms than does *Celebochoerus.* The zygomatic process of the maxillary forms almost a right angle with the surface of the cheek, and the root of the zygomatic process is stated to come as far forward as P^4 (Pilgrim, 1926, pp. 23, 25, pl. VIII). As we see from Pilgrim's plate the contact between M^2 and M^3 is below the zygomatic process of the maxillary, and the anterior margin of the orbit is just above the middle of M^3, as in *Celebochoerus.*

The preorbital fossa shown on the right side of the fossil skull from Celebes is only slightly depressed, and does not have a distinct ridge above, which marks it off from the frontal and nasal regions. In *Sus* and *Potamochoerus* this preorbital fossa is much better defined; the nasals and the anterior portion of the frontals are flattened above and form sharpened edges above the lateral surfaces of the maxillary and the preorbital fossa. This is also the condition that we find in *Propotamochoerus* (Pilgrim, 1926, pl. IX). In *Celebochoerus* there is no evidence of this lateral angulation of the anterior frontal and nasal regions; the sides of the frontals slope evenly outward and pass into the lateral surface of the maxillary without forming any marked edges. In this respect the skull of *Celebochoerus* must have been very different from that of *Sus* or *Potamochoerus,* and it is only in *Phacochoerus* and *Hylochoerus* that we find a condition similar to that in the Celebes fossil suid: the nasals arch from side to side upon the upper surface of the skull and do not show any lateral angulation at all.

I have already remarked above, in connexion with the description of the upper canines, that *Celebochoerus* further agrees with *Phacochoerus* but not with *Hylochoerus* in the development of a heavy tubular alveolus for the upper canine without a longitudinal crest above it. *Celebochoerus* further agrees with these African genera in the anterior divergence of the premolar series and in the outward curve of the palatine grooves between the bases of the canines.

In conclusion, the skull of *Celebochoerus* presents a remarkable combination of characters found in other suid genera; it has the abrupt and rather anteriorly placed zygomatic process of the maxillary of *Propotamochoerus,*

and the transversely arched anterior frontal and nasal regions and the canine alveolus of *Phacochoerus*. These agreements seem to be in the common retention of primitive characters rather than being indications of any real near relationship.

The mandible of *Celebochoerus* can best be studied in the greater part of a right horizontal ramus of the mandible with all the teeth broken off except M_3 (no. 20 in table 9). It shows the alveolus of the canine, and a large mental foramen below the posterior part of P_2. The body of the mandible is rather thick, the lateral surface is convex from above downward, the lower border is thin behind but widens in front, and the medial surface is convex from above downward below the premolars but it becomes concave in its lower part below M_2 and M_3. The concavity of the lower part of the medial surface of the horizontal ramus extends forward only to below the middle of M_2; this is a difference from *Sus* or *Potamochoerus* in which the concavity is more distinctly marked off and elongated anteroposteriorly; it is completely flattened out only below M_1 or even P_4. The pterygoid muscle that inserts into the concave medial surface of the mandibular ramus evidently was less extended at its insertion in *Celebochoerus* than in the modern genera.

The height of the ramus at M_3 is 56 mm, the width at the same level is 30 mm. The maximum width, below M_2, is 33 mm.

A small fragment of the mandible comprises the symphysis, with a pair of large foramina above the prominence behind, at the point of divergence between the rami, larger than I ever saw in a recent suid (pl. I fig. 8). The lower surface of the symphysis as far as preserved (the preserved portion is only that below and between the canine alveoli) is less convex transversely than in *Sus* or *Potamochoerus*, perhaps pointing to a wide and flat mandibular symphysis such as that of *Phacochoerus*, but not enough is preserved to be certain on this point.

POSTCRANIAL SKELETON

Most of the remains of suid bones in the collection from Celebes indicate individuals of rather large size. The best preserved fossil specimens are of the humerus, radius, ulna, unciform, metacarpals III and V, femur, astragalus, and calcaneum, and they will be discussed in that order below. For comparison I used a series of skeletons in the Leiden Museum belonging to the following species: *Sus scrofa* L., *Sus cristatus* Wagner, *Sus barbatus* Müller, *Sus verrucosus* Müller et Schlegel, *Sus celebensis* Müller et Schlegel, *Babyrousa babyrussa* (L.), and *Phacochoerus aethiopicus* (Pallas), all of adult individuals. The measurements of the fossil and recent bones will be found in table 11.

Of the humerus there is a distal fragment, of the left side, comprising the medial condyle and epicondyle. No specific characters can be derived from this fragment except that it exceeds all the available recent specimens in size.

The proximal portion of a left radius, slightly damaged, is wider even than the radius of *Sus strozzii* Meneghini from the Upper Villafranchian of Tegelen, Netherlands, described several years ago (Hooijer, 1947) and preserved in Teyler's Museum at Haarlem. The proximal width of the radius of *Sus strozzii*, 40 mm, is greater than that in any recent radius seen.

More interesting is the distal portion of the radius, for, as pointed out by Stremme (1911, p. 102) it seems possible to distinguish between the *Sus scrofa* group and the *Sus verrucosus* group on the basis of the configuration of the distal articular surfaces of the radius as well as on the shape of the cross section of the lower canines. In *Sus scrofa* and *Sus cristatus* (*vittatus*) the median ridge that separates the facets for articulation with the scaphoid and the lunar respectively is curved in a way different from that found in *Sus verrucosus* and *Sus celebensis*. In the first mentioned species this ridge, emerging in the middle of the anterior edge of the distal surface, runs obliquely backward and inward, then makes a slight inward curve, and then continues running backward and inward over one-half of the width of the bone to the postero-internal corner of the articular surface. In the *Sus verrucosus* group the median distal ridge runs straight backward first, then swings inward for a much longer stretch than in *Sus scrofa*, and curves obliquely backward and inward only close to the medial edge of the articular surface. Consequently, the posterior width of the (medial) scaphoid facet is less relative to that of the (lateral) lunar facet in the *verrucosus* pigs than it is in the *Sus scrofa* group. I have checked this character in the collection available to me, and agree with Stremme as to its validity; the *scrofa* type of distal articular surface of the radius occurs in *Sus cristatus* (both *Sus cristatus cristatus* Wagner from Nepal, and *Sus cristatus milleri* Jentink from Java), while the *verrucosus* type of distal articular surface of the radius is seen in *Sus celebensis* as well as *Babyrousa* and even *Phacochoerus*. The distal portion of the right radius of *Celebochoerus* from Sompoh (pl. V fig. 3) as well as the radius of *Sus strozzii* Meneghini from Tegelen (Hooijer, 1947, p. 41, pl. I figs. 1-2) agree with *Sus verrucosus*, the babirusa, and *Phacochoerus* in the configuration of the distal articular surfaces. The resemblance in this point between such widely divergent types of Suidae is very striking indeed. Unfortunately the only available radius of *Sus barbatus oi* Miller from Sumatra is damaged distally,

but Stremme (1911, p. 102) has already shown that this form has the *verrucosus* type of distal articular surface of the radius.

The distal articular surface of the radius of *Sus strozzii* is 40 mm wide, and measures 23 mm anteroposteriorly, larger than that in any recent suid radius seen by me. The radius of *Celebochoerus,* as will be seen from table 11, is even larger than that of the large *Sus strozzii* of the Upper Villafranchian of Italy, France, and the Netherlands. *Dicoryphochoerus titan* (Lydekker, 1884, p. 64, pl. XII fig. 1) has a radius that also exceeds that of *Sus strozzii* in size; the greatest distal width of the shaft (at the distal lateral expansion in front of the ulna) is 49 mm in *Sus strozzii,* and 60 mm in the radius of *Dicoryphochoerus titan* figured by Lydekker (l.c.); measurements of the distal articular surface of the radius of the latter species are not given. The radius of *Celebochoerus* appears to have been almost as large as that of the giant Siwalik form of *Dicoryphochoerus,* for the greatest width of the fossil fragment is 57 mm, only 3 mm less than that in *Dicoryphochoerus titan* (pl. V fig. 3).

The ulna tells much the same story; the proximal half of a right ulna from Sompoh, with the olecranon and the tip of the processus anconaeus missing, is as wide at the approximal surface for the radius at the level of its glenoid cavity, but more extended anteroposteriorly at the same level as compared with the largest recent ulnae in our collection.

A left unciform from Sompoh is remarkable in that the two articular facets on its medial surface, for the magnum and for the third metacarpal respectively, meet at an obtuse but distinct angle (pl. V fig. 6); in most recent unciforms seen these two medial facets are very much in the same plane. It is only in the two babirusa skeletons and in that of *Phacochoerus* that the magnum and the third metacarpal facets on the unciform meet at an angle of slightly less than 180°; in the remaining skeletons these two facets pass imperceptibly into one another. I have not found any reliable constant difference in the unciform between the *Sus scrofa* and the *Sus verrucosus* groups. It thus appears that the character distinctive of the unciform of *Celebochoerus* is retained, in a less pronounced form, in some of the recent non-*scrofa* suids only.

We have further a complete left third metacarpal (pl. VI fig. 5), the proximal portion of a right third metacarpal, and various distal portions of large metapodials. The metacarpal III is distinguished by its robust build from that of all living Suidae; in table 11 I have given the measurements of the third metacarpals of *Hylochoerus* and *Potamochoerus* as recorded by Bouet and Neuville (1929, p. 230) who describe *Hylochoerus* as having massive and robust metapodials. In the relative width of the shaft *Cele-*

bochoerus exceeds even *Hylochoerus*, which, on the other hand, exceeds *Celebochoerus* in the relative proximal width of the third metacarpal [1]).

There is one complete fifth metacarpal in the Sompoh collection (pl. VI fig. 6) which is very close to that of the recent Suidae compared in the smallish proximal end. Apparently the fifth metacarpal of *Celebochoerus* is in the same reduced state as that in the recent Suidae in which it varies in length from 0.70 to 0.79 of the length of the third metacarpal (table 11). This length ratio is 0.79 for the Sompoh metacarpals but since both are isolated specimens it cannot be made out whether they are from one and the same individual.

Of the femur the collection from Sompoh contains various proximal and distal fragments; the few measurements that can be given point, again, to specimens as large as, or even bigger than the largest of the recent bones.

The astragalus, of which there are six rather complete specimens, all from Sompoh, fall into two size groups, each of three specimens. The larger, one right and two left, might represent males, and the smaller, all of the right side, females, but there is no way of telling the sex of their former owners on the basis of an astragalus as far as I know (pl. VI figs. 8 and 9).

Two portions of the calcaneum, one of the left side, without the extremity that articulates with the cuboid and originating from Tjeleko, and one of the right side, with the tuber missing, from Sompoh, nicely supplement each other, being equally large. Few of the recent calcanea only exceed the Celebes fossil specimens in size. The tuber is deeply grooved posteriorly, and the inner astragaline articular surface is, perhaps, a little less well marked off from the body of the bone than it is in most recent specimens, but this is a minor difference. On the whole the fossil calcaneum agrees well with that of the recent Suidae.

RELATIONSHIPS OF CELEBOCHOERUS

The various distinctive characters of the fossil suid of Celebes have been summarized in the diagnosis which appears on p. 2/3 of the present paper. There are a great number of primitive characters both in the dentition and in the skull of *Celebochoerus* which are retained to a greater or less extent in various living members of the suid family. In the evaluation of all these

1) In connexion with the radius of *Dicoryphochoerus titan* Lydekker (1884, p. 64, pl. XII fig. 2) records the third and fourth left metacarpals the dimensions of which (length of metacarpal III ca. 100 mm, least width of shaft ca. 26 mm) by far exceed those found for *Celebochoerus* or *Hylochoerus*. If they belonged to the same skeleton as the radius, as accepted by Lydekker, *Dicoryphochoerus* had proportionally heavier metapodials than any of the recent suids.

TABLE 11

Measurements of limb and foot bones of *Celebochoerus* and of various recent Suidae

	Celebochoerus heekereni	*Sus scrofa* ♂	*Sus scrofa* ♀	*Sus scrofa* ♀	*Sus cristatus* ♂	*Sus cristatus* ♀	♀ *Sus barbatus oi*	♂ *Sus verrucosus*	♂ *Sus celebensis*	♂ *Babyrousa babyrussa*	♀ *Babyrousa babyrussa*	♀ *Phacochoerus*	*Phacochoerus*	*Hylochoerus*	*Hylochoerus*	*Potamochoerus*
Humerus, distal ant. post. diam., medial side	64	—	35	49	50	32	44	35	31	36	34	41				
Radius, proximal width	44+	29	31	37	36	23	29	25	24	29	25	32				
Width of distal articular surface	49	29	26	36	34	23	—	26	25	28	24	31				
Ant. post. diam. of idem	29	19	17	22	22	14	—	16	14	18	14	18				
Ulna, width of ant. surface at level of glenoid cavity of radius	31	24	20	29	29	17	22	19	22	23	20	24				
Greatest diameter at same level	41	29	27	36	32	21	27	24	25	28	23	28				
Unciform, width of ant. surface	26	19	18	24	22	15	21	17	16	17	15	20				
Height of idem	22	16	14	20	20	13	18	14	13	14	14	15				
Greatest dorso-volar diameter	37	28	24	32	33	21	29	22	23	24	21	25				
Metacarpal III, greatest length	76	76	68	83	84	67	83	71	64	71	63	77	60	87	82	71
Proximal width	25	24	21	27	27	17	22	19	19	19	17	25	19	33	31	21
Distal width	21	17	16	20	19	13	20	16	14	14	15	17	16	25	22	18
Least width of shaft	19	16	14	18	17	11	18	14	12	13	13	16	12	20	18	11
Least ant. post. diameter of idem	14	10	10	13	11	8	12	10	8	9	10	11	8	14	12	10
Ratio: proximal width: length	0.33	0.32	0.31	0.33	0.32	0.25	0.27	0.27	0.30	0.27	0.27	0.32	0.32	0.38	0.38	0.30
Ratio: shaft width: length	0.25	0.21	0.21	0.22	0.20	0.16	0.22	0.20	0.19	0.18	0.21	0.21	0.20	0.23	0.22	0.15
Metacarpal V, greatest length	60	60	54	61	66	47	64	50	46	51	47	59				
Distal ant. post. diam. of idem	18	15	13	18	18	12	16	13	11	14	13	14				
Ratio: length mcV: mcIII	—	0.79	0.79	0.73	0.79	0.70	0.77	0.70	0.72	0.72	0.75	0.77				
Femur, proximal width over caput and trochanter major	82	64	—	68	72	47	55	53	52	59	54	61				
Distal ant. post. diam., medial side	74	66	58	72	76	50	63	51	48	50	49	61				
Astragalus, lateral length	46-47, 53-55	43	39	53	55	36	43	39	34	38	36	42				
Distal width of idem	26-28, 31-32	26	22	33	28	21	23	23	19	21	20	24				
Calcaneum, length from tuber to base of inner astragaline art. surface	62	57	56	70	67	51	56	56	49	57	50	58				
Ant. post. diam. at level of inner astragaline art. surface	27	23	21	28	29	19	23	20	19	21	19	22				

characters, with the aim to determine the position of *Celebochoerus* in the phylogenetic classification of the Suidae there is a strong personal element. One has only to compare Pilgrim's phylogeny of the Indian Suidae (Pilgrim, 1926, pl. I) with that later presented by Colbert (1935a, p. 9) to become aware how much the ideas of different students about the same material may differ. I propose to follow Colbert, whose idea is that the pigs did not begin their adaptive radiation until some time in the Oligocene.

By Miocene times (Kamlial of the Siwaliks) the *Propotamochoerus- Potamochoerus* group had already split off, and so had the *Conohyus* line which latter gave rise to *Sivachoerus* and *Tetraconodon*. We have *Sivachoerus* in the Astian of Wadi Natrun in Egypt, and in what are probably synchronous deposits at Sahabi in Cyrenaica (Tobien, 1936; Leonardi, 1952). In our *Celebochoerus* there is no enlargement of the premolars as seen in the *Conohyus-Sivachoerus-Tetraconodon* group; all in all the genus *Celebochoerus* seems to be most closely related to the *Potamochoerus* group. *Celebochoerus,* however, differs from *Propotamochoerus* in a combination of primitive and progressive characters; it is more primitive than *Propotamochoerus* in the lower premolars which are less elevated anteriorly and posteriorly, and in the absence of lateral angulation of the anterior frontal and nasal regions, while it is more progressive than *Propotamochoerus* in the loss of P_{1-2}.

Consequently, the relationships of *Celebochoerus* probably are best stated thus: it is a collateral development of *Propotamochoerus* from the same ancestral stock. This would point to an independent development of *Celebochoerus* since the Miocene, whereby it preserved the *verrucosus* lower canine and generalized molar structure of the earlier Suidae, at the same time developing the large upper canines without much or any enamel that form its most distinctive specialization among fossil and recent Suidae, and of which we find a parallel only in the living African *Phacochoerus*.

There is no evidence of any real near relationship with either of the two forms of Suidae today living in Celebes, *Sus celebensis* and *Babyrousa babyrussa*. *Celebochoerus* as it existed in the Pleistocene of Celebes is the result largely of long independent evolution such as may occur in isolated regions like the island of Celebes. The babirusa is a different product of the same evolutionary forces, one that outlived *Celebochoerus* and survives until today. Both of these genera preserved the generalized molar structure and potamochoeroid premolars but differed widely in the specialization of their canine teeth.

AGE AND COMPOSITION OF THE ARCHIDISKODON-CELEBOCHOERUS FAUNA

The geological age of the *Archidiskodon-Celebochoerus* fauna can be provisionally regarded as Pleistocene, Early Pleistocene at most as attested by *Archidiskodon celebensis,* a pygmy species of the *Archidiskodon planifrons* group that characterizes the Early Pleistocene in Asia as well as in Europe and North Africa. A further hint as to the geological age of the Tjabengè fauna is given by the associated flake culture, which is similar to the Sangiran culture of the Upper Pleistocene Notopuro beds of Java. It would be rash, however, to conclude from the identity of two flake cultures in different regions that these cultures are synchronous. The Sangiran culture of Java is associated with very advanced *Stegodon* as well as *Elephas,* not with primitive archidiskodonts such as *Archidiskodon celebensis.* Unfortunately the Tjabengè *Stegodon* is not preserved well enough to be of much use as a time marker.

Some faunal stratification at Tjabengè is evident as the extinct species of mammals that occur there either belong to genera that are found elsewhere in the Pleistocene of Asia (*Stegodon, Archidiskodon*), or are endemic even as to genus (*Celebochoerus*). The ancestor of *Celebochoerus* would seem to have entered Celebes earlier than that of *Archidiskodon celebensis* because the former is more differentiated, more distinctive of the fauna of the island, than *Archidiskodon celebensis.*

Babyrousa is another endemic [1]) suid genus of Celebes. As I have noted above in connexion with the description of the molars of *Celebochoerus,* which appeared to be indistinguishable from those that I have ascribed to a fossil race of babirusa (Hooijer, 1948c), the presence of *Babyrousa* in the *Archidiskodon-Celebochoerus* fauna lacks convincing proof. However, if babirusa did not actually occur at Tjabengè it is more probable than not that it already existed, either in Celebes or elsewhere, at the time of the *Archidiskodon-Celebochoerus* fauna.

If the babirusa has not come as such from another region (and there is nothing to support this view as we do not know of any fossils outside Celebes that represent the babirusa or a possible immediate ancestor) the babirusa is autochthonous in Celebes. It should, then, have existed in Celebes for a length of time sufficient for its generic differentiation to have taken place. It seems improbable that this transformation has occurred in the

1) Not strictly endemic since it also lives in the Sula islands and in Buru. It is probable, however, that the babirusa was brought to Buru by Man (Dammerman, 1929, p. 154).

relatively short time span of the Pleistocene. Thus, always assuming that babirusa is autochthonous in Celebes, this genus would seem to have been in existence already at the time of the *Archidiskodon-Celebochoerus* fauna, and we might discover its remains, if we do not already have, at Tjabengè or at some Pleistocene site elsewhere in Celebes.

The *Archidiskodon-Celebochoerus* fauna as we now know it is of an impoverished, unbalanced type as compared with the rich Pleistocene faunas of India, Burma, China, or Java, such as we could expect to be the result of waif dispersal of the ancestral forms to the island of Celebes over a great length of time. It seems unlikely that we have found all the elements to the Tjabengè fauna, but certainly we know its most common species. Exactly when the various ancestral forms did spread into the island, and where they came from, are problems that only future research eventually may solve.

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EXPLANATION OF THE PLATES

Plate I

Celebochoerus heekereni Hooijer, Sompoh, S. W. Celebes; figs. 1-2, P_3-M_3 sin.; fig. 1, crown view; fig. 2, buccal view; fig. 3, right ramus of the mandible with M_{1-3}, crown view; fig. 4, P_{3-4} dext. (no. 9), lingual view; fig. 5, P_{3-4} dext. (no. 10), lingual view; fig. 6, P_{3-4} dext. (no. 11), lingual view; fig. 7, right ramus of the mandible with P_4 and M_2, crown view; fig. 8, symphysis of mandible, upper view; fig. 9, tip of upper C dext., posterior view; fig. 10, lower C dext. (no. 1), anterior view (the internal surface is to the left, the posterior surface above in the figure); fig. 11, upper C sin., anterior upper view.

All figures natural size.

Plate II

Celebochoerus heekereni Hooijer, Sompoh (except figs. 10 and 19), S.W. Celebes; figs. 1-2, P_4 dext. (no. 2); fig. 1, lingual view; fig. 2, crown view; figs. 3-4, P_4 sin. (no. 6); fig. 3, buccal view; fig. 4, crown view; figs. 5-6, P_4 dext. (no. 7); fig. 5, lingual view; fig. 6, crown view; figs. 7-8, P_4 dext. (no. 8); fig. 7, lingual view; fig. 8, crown view; fig. 9, P_{3-4} dext. (no. 9), crown view; fig. 10, P_4 sin. (no. 3), Tjeleko, crown view; fig. 11, P_4 dext. (no. 4), crown view; fig. 12, M_3 dext. (no. 6), crown view; fig. 13, M_3 dext. (no. 7), crown view; fig. 14, M_3 dext. (no. 8), crown view; fig. 15, M_3 dext. (no. 9), crown view; fig. 16, M_3 sin. (no. 21), crown view; fig. 17, M_3 sin. (no. 22), crown view; fig. 18, M_3 sin. (no. 23), crown view; fig. 19, M_3 sin. (no. 24), Beru, crown view.

All figures $1^1/_2$ natural size.

Plate III

Celebochoerus heekereni Hooijer, Sompoh (except figs. 5 and 10), S.W. Celebes; figs. 1 and 4, I_{1-2} sin; fig. 1, lingual view; fig. 4, labial view; figs. 2-3, I_1 dext.; fig. 2, lingual view; fig. 3, labial view; fig. 5, I^1 sin. (no. 11), Tjeleko, labial view; fig. 6, M^3 dext. (no. 9), crown view; figs. 7-8, I^1 dext. (no. 10); fig. 7, posterior lower view; fig. 8, labial view; fig. 9, P^4 dext. (no. 33), crown view; fig. 10, I^1 sin. (no. 11), Tjeleko, posterior lower view; fig. 11, M^3 dext. (no. 24), crown view; fig. 12, P^2 dext., crown view; fig. 13, P^3 dext. (no. 4), crown view; fig. 14, P^4 dext. (no. 5), crown view; fig. 15, P^4 dext. (no. 13), crown view; fig. 16, M^3 dext. (no. 18), crown view; fig. 17, P^4 dext. (no. 5), buccal view; fig. 18,

I^3 dext. (no. 5), crown view; figs. 19-20, P^3 dext. (no. 3); fig. 19, lingual view; fig. 20, crown view; fig. 21, P^4 dext. (no. 34), crown view; fig. 22, P^4 sin. (no. 40), crown view; figs. 23-24, P^3 dext. (no. 2); fig. 23, lingual view; fig. 24, crown view.

All figures $1^1/_2$ natural size.

Plate IV

Celebochoerus heekereni Hooijer, Sompoh (except fig. 5), S. W. Celebes; fig. 1, tip of upper C dext., upper view; fig. 2, tip of upper C dext., upper view; fig. 3, upper C dext. (no. 4), anterior upper view; fig. 4, upper C sin. (no. 6), anterior view; fig. 5, upper C dext. (no. 5), Beru, upper view; fig. 6, upper C sin. (no. 7), anterior upper view.

All figures natural size.

Plate V

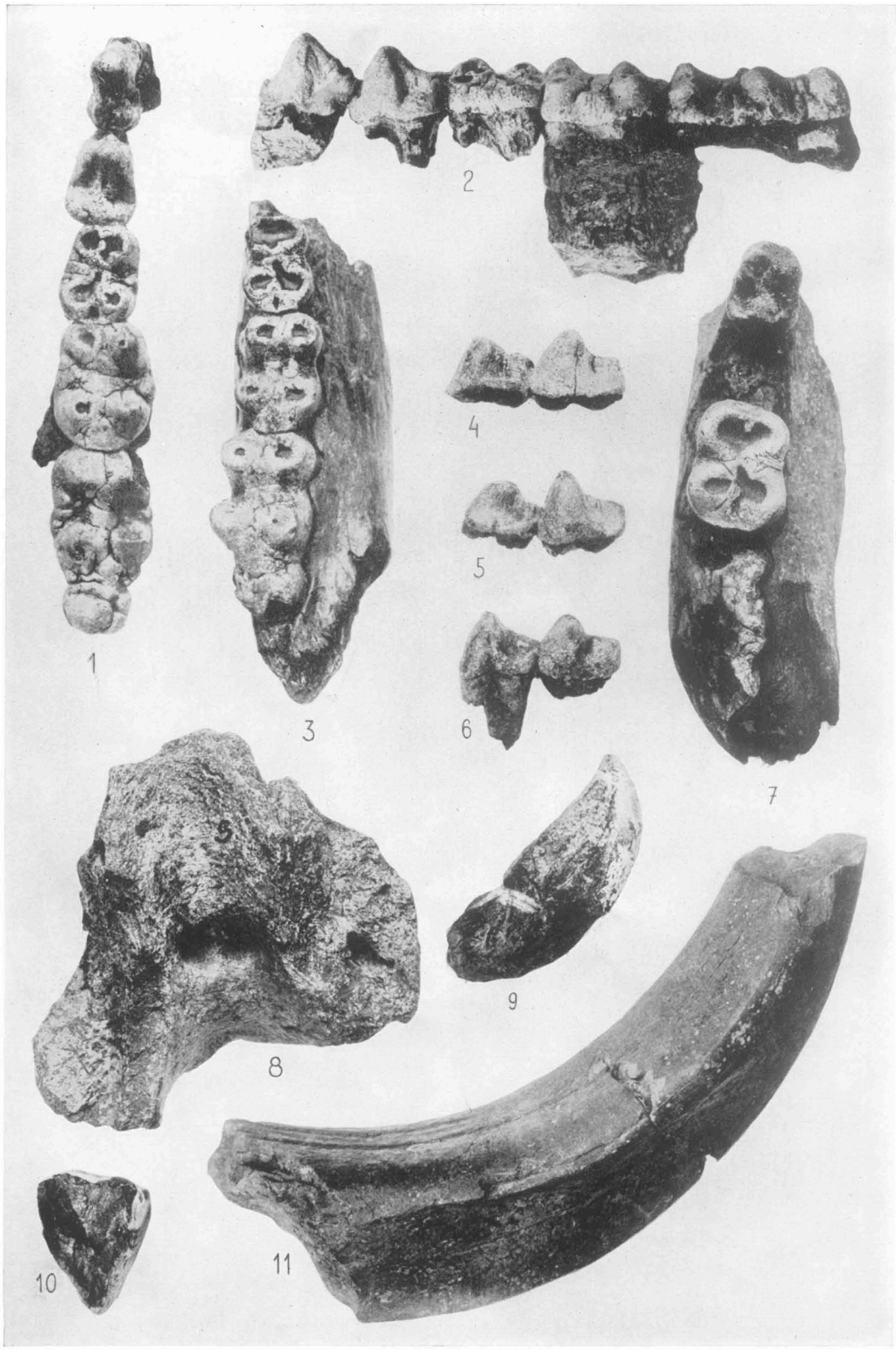
Celebochoerus heekereni Hooijer, Sompoh, S. W. Celebes; fig. 1, upper C dext. with the tip entire, anterior view; fig. 2, upper C dext. (no. 1), proximal view (the anterior surface is to the left, the upper surface above in the figure); fig. 3, radius dext., distal view; fig. 4, upper C sin. (no. 66), anterior view; fig. 5, upper C dext. (no. 53), anterior view; fig. 6, unciform sin., anterior view; fig. 7, M^{1-3} dext., crown view.

All figures natural size.

Plate VI

Celebochoerus heekereni Hooijer, Sompoh (except figs. 1-2), S.W. Celebes; figs. 1-2, left maxillary with base of C, and P^{2-4} partially preserved, Tjeleko; fig. 1, palatal view; fig. 2, anterior view, showing absence of jugum caninum; fig. 3, right maxillary with P^3-M^2 (partim), palatal view; fig. 4, upper C sin. (no. 2), proximal view (the anterior surface is to the right, the upper surface above in the figure); fig. 5, metacarpal III sin., anterior view; fig. 6, metacarpal V sin., anterior view; fig. 7, upper C dext. (no. 53), proximal view (the anterior surface is to the left, the upper surface above in the figure); fig. 8, astragalus dext. (smaller type), anterior view; fig. 9, astragalus dext. (larger type), anterior view.

All figures natural size.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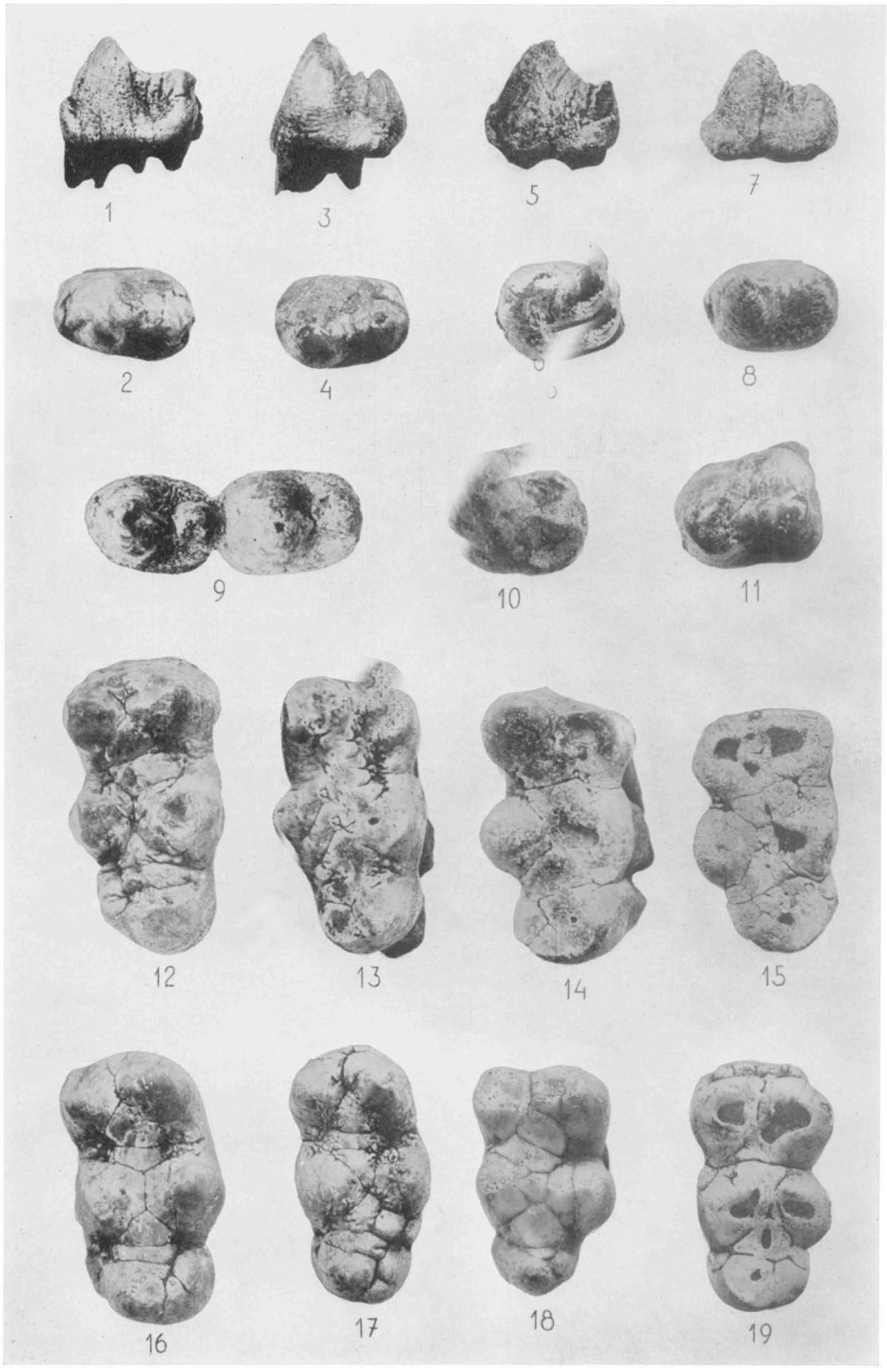
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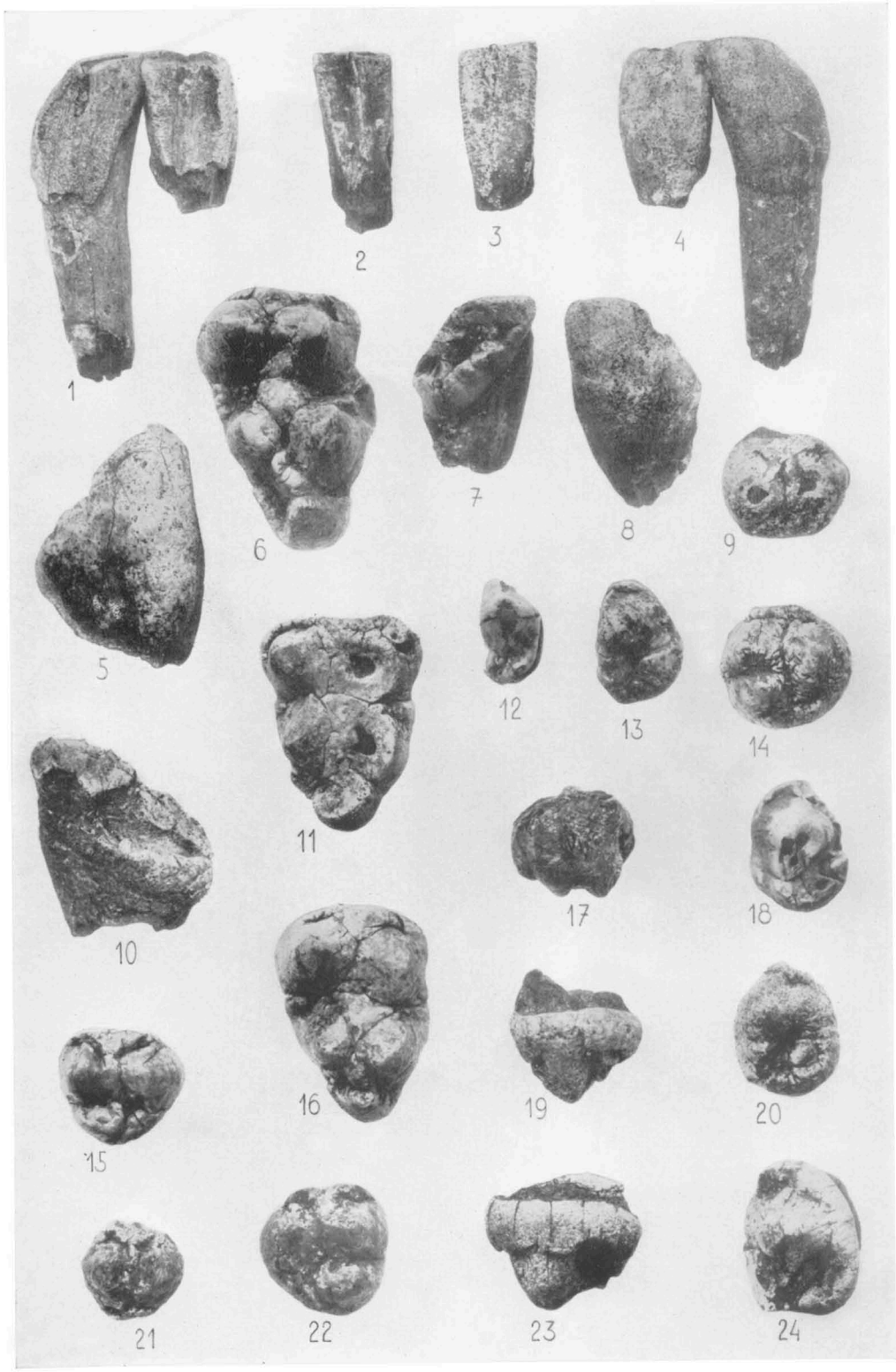
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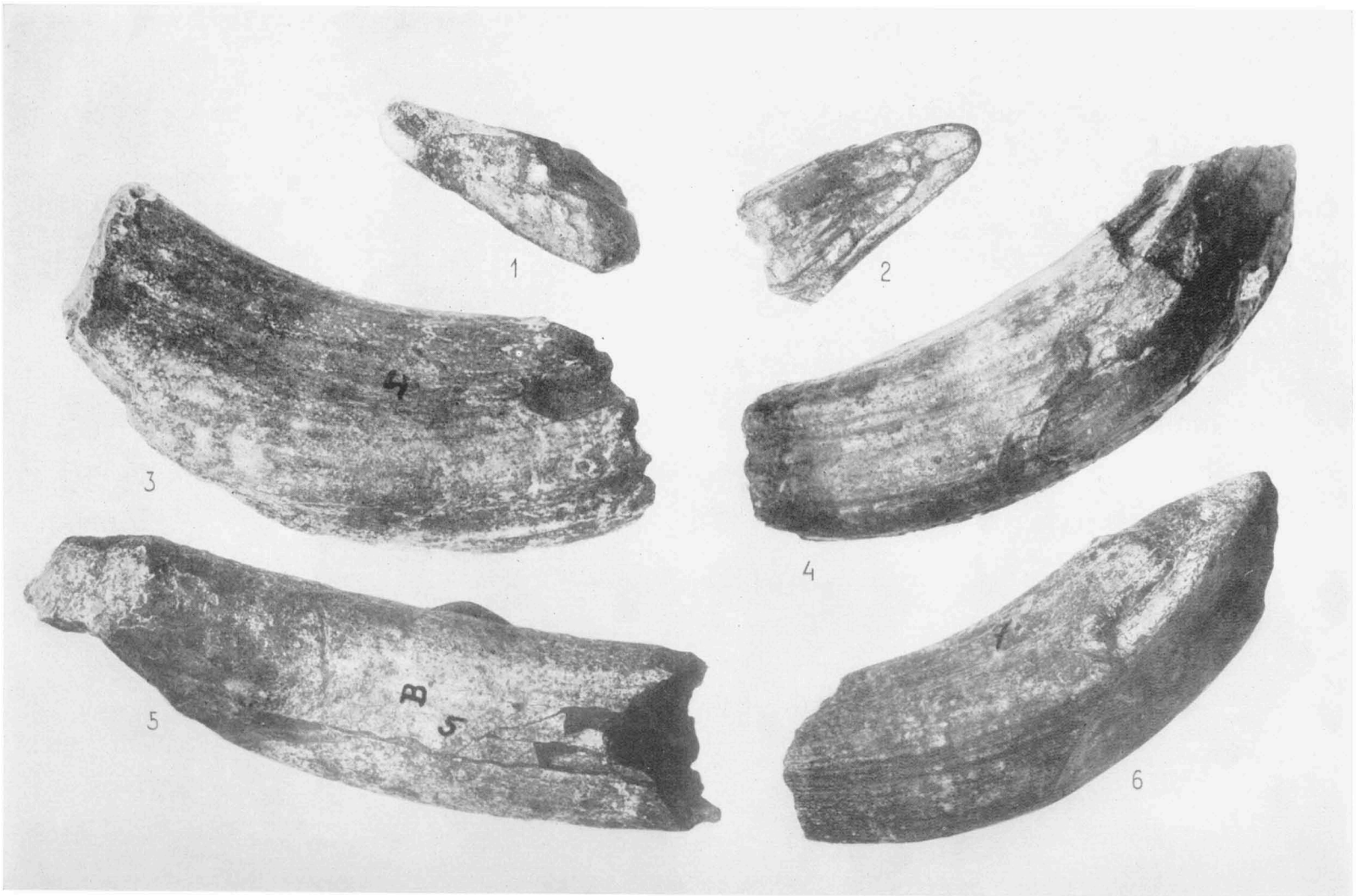
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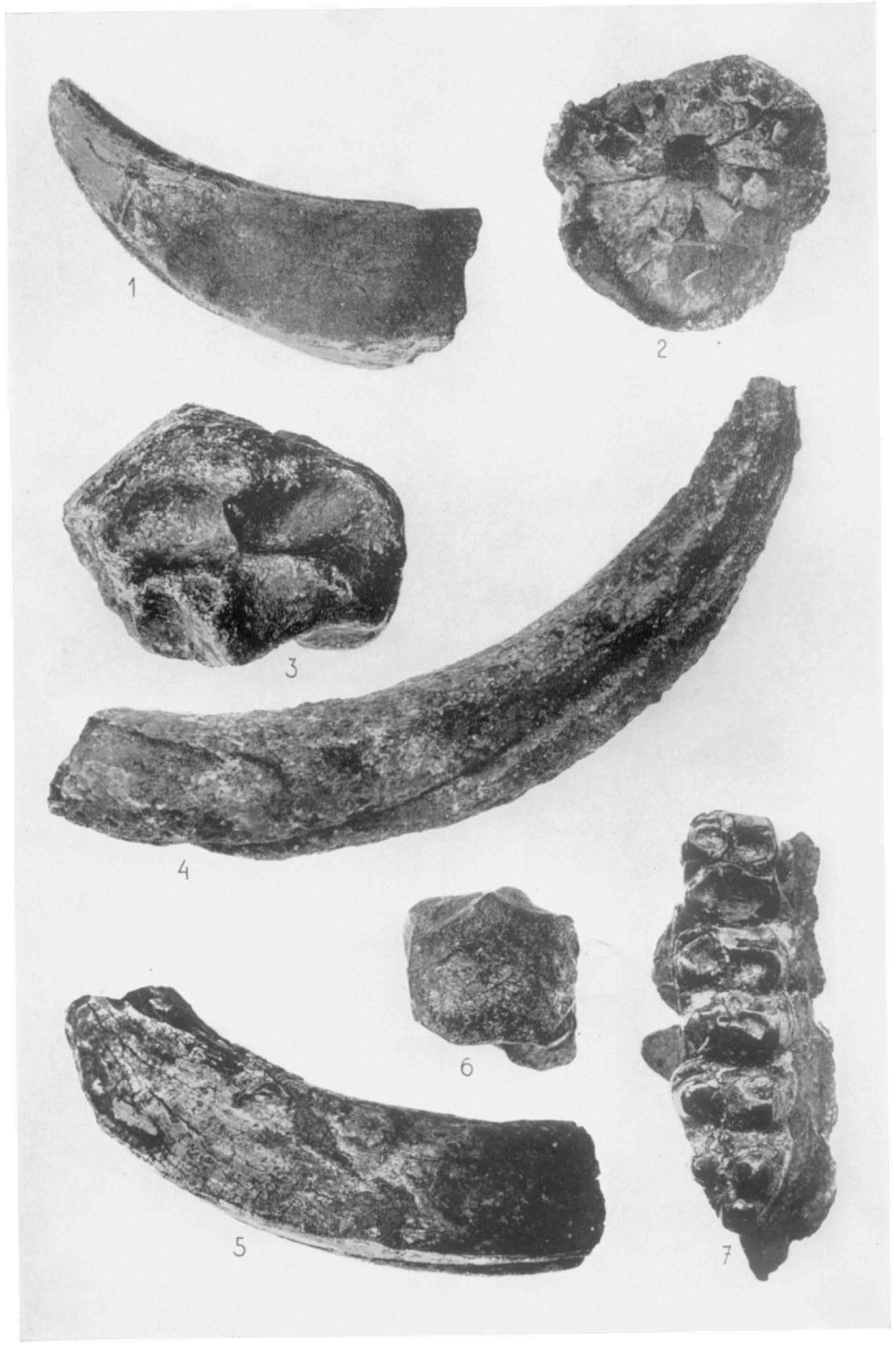
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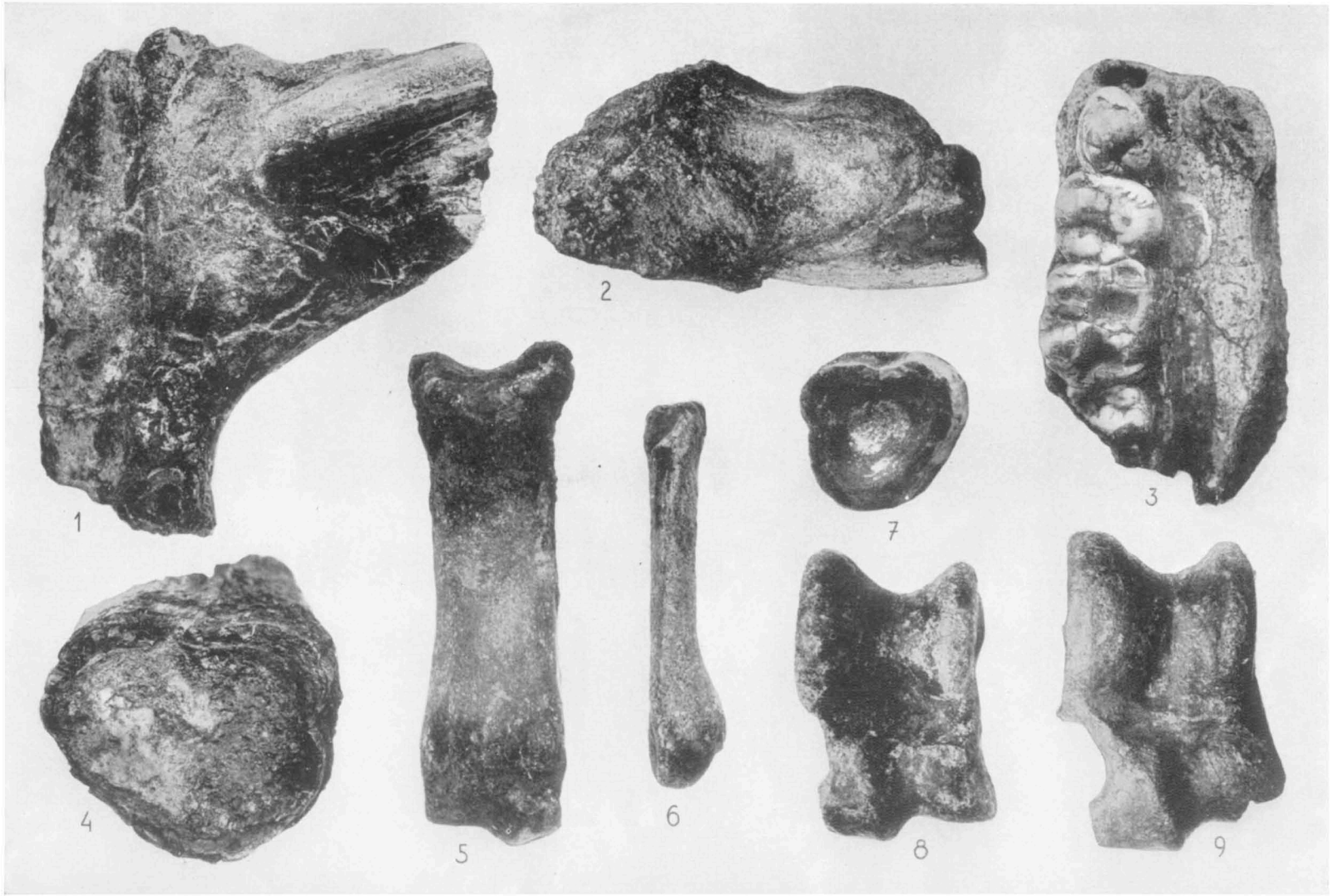
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