FOSSIL BOVIDAE FROM THE MALAY ARCHIPELAGO AND THE PUNJAB

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with pls. I-IX

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INTRODUCTION

The Bovidae make up a very large portion of the Dubois collection of fossil vertebrates from Java, second only to the Proboscidea in bulk. Before Dubois began his explorations in Java in 1890 we knew very little about the fossil bovids of that island. Martin (1887, p. 61, pl. VII fig. 2) described a horn core as *Bison sivalensis* Falconer (?); *Bison sivalensis* Martin has already been placed in the synonymy of *Bibos palaesondaicus* Dubois by Von Koenigswald (1933, p. 93), which is evidently correct. Pilgrim (in Brongersma, 1936, p. 246) considered the horn core in question to belong to a *Bibos* species closely related to the banteng. Two further horn cores from Java described by Martin (1887, p. 63, pl. VI fig. 4; 1888, p. 114, pl. XII fig. 4) are not sufficiently well preserved to allow of a specific determination, although they probably belong to *Bibos palaesondaicus* Dubois as well.

In a preliminary faunal list Dubois (1891) mentions four bovid species as occurring in the Pleistocene of Java, viz., two living species (the banteng and the water buffalo) and two extinct forms, *Anoa* spec. nov., and *Bos* (or *Bison?*) spec. nov. The alleged *Anoa* was named *Anoa santeng* Dubois (in Jentink, 1891), but later renamed *Tetraceros kroesenii* Dubois (1907). The *Bos* or *Bison* was found to be a *Leptobos* (Anonymus, 1892). In his 1908 survey of the fossil vertebrate fauna of Java Dubois enumerates six species of Bovidae, all but the first of them new to science, as follows:

Tetracerus kroesenii,
Leptobos groeneveldtii,
Leptobos dependicornus,
Bibos palaesondaicus,
Bibos protocavifrons, and
Bubalus palaeokerabau.

Stremme (1911) raised *"Tetracerus" kroesenii* to distinct generic rank, *Duboisia,* and added very materially to our knowledge of some of the forms named by his descriptions and figures of skull and dentition of *Duboisia santeng, Bibos palaesondaicus,* and *Bubalus palaeokerabau.* The collection of the Selenka expedition to Trinil studied by Stremme does not contain any material of *Leptobos,* and none of *Bibos protocavifrons* either. Soergel (1913) records a skull from Kedoeng Loemboe (Elbert collection) answering the description of *Bibos protocavifrons*; however, he does not provide any description or figure. In his work on the Limbangan fauna Stehlin (1925) gives a description of a horn core most probably belonging to Dubois's *Leptobos groeneveldtii,* and further mentions fragmentary remains of large bovids as well as of an antelope.

Descriptions and figures of fossil skulls of banteng and water buffalo from various localities in Java have been given by Van der Maarel (1932). Van der Maarel considers his fossil material to be conspecific with the living forms but is careful in stating that in the absence of any figures of Dubois's specimens he is unable to determine whether Dubois's species of *Bibos* and *Bubalus* are valid and distinct from the recent species.

In the opinion of Von Koenigswald (1933, 1934) *Bibos palaesondaicus* and *Bubalus palaeokerabau* are only subspecifically distinct from the extant species. Three of Dubois's new species, viz., *Leptobos groeneveldtii, L. dependicornus,* and *Bibos protocavifrons,* are declared "nomina nuda". Five names are added to the list of Pleistocene Java Bovidae, viz., *"Antilope" gracilicornis* Von Koenigswald (1933, p. 82), *Antilope modjokertensis, Antilope saätensis,* and *Leptobos cosijni* Von Koenigswald (1934, pp. 192 and 193), and, finally, *Probibos djulangensis* Von Koenigswald (1950, p. 92). The first and the last of these should be kept on the paleontological suspense account: the battered skull on which *"Antilope" gracilicornis* is based may be cervid rather than bovid in characters (the poor figure does not permit of a decision one way or the other), while the only diagnosis of *Probibos djulangensis* available to date is: "The jaw is about two third the size of a Bibos jaw; the dentition suggests a relation with that group".

Both of *Antilope modjokertensis* and of *Antilope saätensis* generic allocation is admittedly provisional; in the absence of horn cores the genus cannot be determined (Von Koenigswald, 1934, p. 192). Hence, there is no justification for placing *Antilope,* a genus of Pallas, 1766, today confined to a single Indian species, *Antilope cervicapra* (Linnaeus), on the list of fossil genera of Java as done by Von Koenigswald (1940, p. 71). It would have been less confusing if Von Koenigswald had introduced his supposedly new species as "Genus indet. (cf. *Antilope*) *modjokertensis* nov. spec.", and "Genus indet. (cf. *Antilope*) *saätensis* nov. spec."; it seems quite legitimate to describe new species the genus of which is indeterminate (see, e.g., Pilgrim, 1939, pp. 36, 40, 42, 57, 86, 107, and 114).

It is Von Koenigswald's opinion that *Duboisia santeng* occurs only in the Trinil beds, whereas his Modjokerto antelope would be confined to the underlying Djetis beds. Likewise, *"Bos (Bibos) banteng palaeosondaicus* Dubois" and *"Bos (Bubalus) bubalis palaeokerabau* Dubois" are found in the Trinil beds, and *"Leptobos cosijni"* in the Djetis beds. The stratigraphical position of *"Antilope saätensis"* is uncertain (Von Koenigswald, 1934, p. 192/193). However, a single referred specimen was found at Sangiran I (Djetis beds) (*Antilope* cf. *saätensis*: Von Koenigswald, 1934, p. 193, pl. III fig. 8; refigured as *Antilope saätensis* in Von Koenigswald, 1940, pl. II fig. 5). Thus, Von Koenigswald would have us believe that *"Antilope"* and *Leptobos* are from the Djetis, and *Duboisia, Bibos,* and *Bubalus* from the Trinil beds (see Von Koenigswald, 1940, p. 61).

There is a great deal to say respecting this matter, not only as regards the correct identification of the bovid types of Dubois and of Von Koenigswald as to genus and species and the synonymies involved, but also as regards the stratigraphical side of the question. Let us first consider systematically how many of Dubois's new species are valid, then go on to Von Koenigswald's new species, and finally look into the stratigraphic evidence adduced by Von Koenigswald.

The fact that Dubois (1908) gave only brief diagnoses of his new species and no figures at all is no reason to consider these names invalidly published. Stremme (1911), whose excellent report on the Selenka Trinil collection is still the best work on the mammalian fauna of the Trinil beds as a whole, found Dubois's species often strikingly well characterized. "So skeptisch ich anfangs den Bestimmungen der Säugetiere bei Dubois gegenüberstand, so musste ich doch auf die Dauer fast in allen Fällen seinen Ansichten zustimmen" (l.c., p. 82/83). As far as *Duboisia* is concerned there can be no doubt that the material described by Stremme is identical with Dubois's *Tetraceros kroesenii*. Moreover, this has been confirmed by Dubois when visiting the Selenka collection at Berlin (Stremme, l.c., p. 123). The skulls found by Dubois and first described and figured in the present paper resemble that dealt with by Stremme in every detail. Since Dubois explicitly states that his *Tetracerus kroesenii* is the same species as that originally named *Anoa santeng* (Dubois, 1908, p. 1260, footnote 1), and since it is clearly stated in the paper by Jentink (1891) that the description of *Anoa santeng* was prepared by Dubois, the correct name of this, the only known species of *Duboisia* Stremme, is *Duboisia santeng* (Dubois). The water buffalo, a fine skull of which has been described by Stremme (1911) as *"Buffelus palaeokerabau* Dubois" doubtless is identical with *Bubalus palaeokerabau* of Dubois's (Stremme, l.c., p. 135), and should be so named; *Bubalus* Smith, 1827, has 38 years' priority over *Buffelus* Rütimeyer (Pilgrim, 1939, p. 254).

In his paper of 1908 Dubois named two species of *Bibos* with the new specific names *palaesondaicus* and *protocavifrons* respectively. In the handwritten catalogue of specimens of his collection preserved in the Leiden Museum Dubois even added a third new specific name, for a *Bibos* skull collected at Trinil in 1900 (Coll. Dub. no. 2774), but this name has never been published by Dubois and will also be omitted by me in order to keep the synonymy as simple as possible. As it happens, the synonymy of the fossil banteng of Java is complicated enough already for Dubois thrice gave a name to one and the same species. Not only do *Bibos palaesondaicus* Dubois (1908, p. 1262), type skull from Trinil (Coll. Dub. no. 2798) found in 1900, and *Bibos protocavifrons* Dubois (1908, p. 1262), type skull found at Tegoean in March, 1891 (Coll. Dub. no. 2797) refer to the same species, but Dubois's second species of *"Leptobos"*, *L. dependicornus* Dubois (1908, p. 1261/1262), type skull from Trinil, 1900 (Coll. Dub. no. 2812), likewise is a *Bibos*; it represents the female of *Bibos palaesondaicus* Dubois. Although *Leptobos dependicornus* has line precedence over *Bibos palaesondaicus* as well as over *Bibos protocavifrons* the three names were published in the same paper and on the same date. I select *Bibos palaesondaicus*, to the exclusion of the others, as the name to be used for the fossil banteng of Java because this name has been in use ever since it was first published, while the status of *Leptobos dependicornus* and of *Bibos protocavifrons* has never been well understood. It is a curious coincidence that Dubois considered *Leptobos dependicornus* to be the female of his *Leptobos groeneveldtii* while in reality it is the female of his

Bibos palaesondaicus. The first skull of *Bibos palaesondaicus* to have been described, viz., that of Stremme (1911, pl. XX figs. 10-11) is that of a female, too.

There remains only one of Dubois's new species to be discussed: *Leptobos groeneveldtii* Dubois (1908, p. 1261), type skull from Wadegan (Coll. Dub. no. 2766). A brief description of this skull as well as some measurements are contained in Pilgrim's monograph on the fossil Bovidae of India (Pilgrim, 1939, pp. 307 and 308). Though some of Pilgrim's observations and measurements are evidently wrong, and will be corrected in the present paper, Pilgrim did not fail to observe that the Java *Leptobos* "in almost every one of its characters shows a distinct advance on *L. falconeri* and to a somewhat less degree on the European species of the genus" (l.c., p. 307). My study of the entire Dubois collection material, and extensive comparisons with *Leptobos falconeri* Rütimeyer of the Upper Siwaliks (British Museum (Natural History) collection) as well as with species of *Leptobos* from Europe has convinced me that *Leptobos groeneveldtii* Dubois represents a decidedly more progressive stage than any of the other species of *Leptobos.* For this reason I have raised Dubois's species to distinct generic rank: *Epileptobos* (Hooijer, 1956b). A detailed description of the material from Java as well as of *Leptobos falconeri,* the genotype of *Leptobos* proper, will be found in the systematic part of the present paper.

The only synonym of *Epileptobos groeneveldtii* (Dubois) is *Leptobos cosijni* Von Koenigswald (1934); the skull figured as *L. cosijni* has all the characters of *Epileptobos* and doubtless is identical with the Dubois collection material. This fact has also been alluded to by Pilgrim (1939, p. 303).

I have already pointed out that two of Von Koenigswald's new species, viz., *"Antilope" gracilicornis* and *Probibos djulangensis,* need not concern us at present as they are insufficiently known or described. There remain the two species of *"Antilope"* named *modjokertensis* and *saätensis* respectively. The former, as will be shown in the present paper, is a true *Duboisia,* conspecific with *Duboisia santeng* (Dubois). Of *"Antilope" saätensis* there does not appear to be any material in the Dubois collection or in others that I have been able to examine; notes relating to Von Koenigswald's material will be found in the chapter on *Duboisia* (p. 18).

The Dubois collection contains material from a great many sites in Java but dates from the years 1890 to and including 1900, long before any attempt had been made to build up a Pleistocene stratigraphy of the Kendeng beds. We owe such a stratigraphy to Von Koenigswald (1934, 1935a), who, in collaboration with the Geological Survey, established what in his opinion is a threefold division of the Pleistocene vertebrate-bearing strata: the Djetis beds with an early Pleistocene fauna, typically from the Poetjangan deposits near Djetis, North of Modjokerto in Eastern Java, the Trinil beds with a Middle Pleistocene fauna, typically from the Kaboeh deposits at Trinil, West of Ngawi, Central Java, and the Ngandong beds with an Upper Pleistocene fauna, typically from high terraces North of Ngawi. Several older faunas have also been distinguished, one from the Tjidjoelang, South of Cheribon, Western Java, and one from the Kali Glagah near Boemiajoe, South of Tegal, Western Java. The Tjidjoelang and the Kali Glagah faunas have been placed in the Middle and the Upper Pliocene, respectively, by Von Koenigswald, but in this he is not followed by Colbert (1942, p. 1454; 1943, p. 426), Movius (1944, p. 84; 1955, p. 260), and myself (Hooijer, 1950, p. 37, footnote 1; 1951, p. 272; 1952, p. 441; 1955, p. 4; 1956c; 1956d, p. 6; 1957, p. 5). It is because of the presence of Villafranchian forms, notably *Archidiskodon,* in the Tjidjoelang and Kali Glagah faunas that these must be assigned a place in the Early Pleistocene, as fully set forth in all the papers referred to above. As far as the Bovidae are concerned the Tjidjoelang fauna contains only antelopes and *"Probibos djulangensis"* (Von Koenigswald, 1950, p. 92), whereas in the Kali Glagah fauna we find only the nondescript *"Antilope gracilicornis"*, and a *"Bubalus"* (Von Koenigswald, 1935a, p. 194); *"Bos* sp." (Von Koenigswald, 1950, p. 92).

The Djetis fauna, as I have pointed out before (Hooijer, 1952, p. 439; 1954, p. 91/92; 1955, p. 5; 1956d, p. 7; 1957, p. 7) is not Early, but Middle Pleistocene in age because it contains various invading elements from the Middle Pleistocene *Stegodon-Ailuropoda* block, a post-Villafranchian mammalian assemblage widely spread in Southeastern Asia the typical development of which is in Southern China (Young and Liu, 1951; Colbert and Hooijer, 1953). The Trinil fauna sensu stricto is likewise Middle Pleistocene, as generally agreed upon by all recent workers in the field.

Although less important stratigraphically than the proboscideans (see Hooijer, 1955, pp. 3-8) the bovids also have a bearing on the problem of the age of the beds in which they occur. *Leptobos* is one of the characteristically Villafranchian elements; it is even the only bovine in the Villafranchian of Europe (Pilgrim, 1938, pp. 451, 466; 1944, p. 29). In the Pinjor zone of the Upper Siwaliks it also exists, likewise in a Villafranchian context (*Leptobos falconeri* Rütimeyer: Pilgrim, 1939, p. 305). *Leptobos* does not occur in post-Villafranchian deposits; the record of *Leptobos* from the Middle Pleistocene Narbada beds (*Leptobos* (*Bibos*?) *frazeri* Rütimeyer, 1878, p. 165) is erroneous, for, as Duerst (1926, pp. 135-137) and Pilgrim (1939, p. 319) have shown, the skull in question belongs to *Bos namadicus* Falconer instead. Over in Europe, the teeth from Süssenborn, early post-Villafranchian in age, referred to *Leptobos* by Wüst (1901, pl. IX), an identification considered doubtful by Pilgrim (1939, p. 304), are too hypsodont and too large for *Leptobos* (Schreuder, 1945, p. 163; 1949, p. 353).

In the Villafranchian of Java, represented by the Tjidjoelang and the Kali Glagah faunas, no *Leptobos* has ever been found, or if it has, no description is available. From the Djetis beds of Java Von Koenigswald (1934, p. 193, pl. III figs. 1-2) has recorded his *"Leptobos cosijni"*, but this is not a Villafranchian *Leptobos,* and represents a much more advanced stage: *Epileptobos groeneveldtii* (Dubois). There is some material of this form, including the highly characteristic skull top, in the collection made near Djetis and Perning North of Modjokerto, Eastern Java, by Cosijn (1931, 1932), a collection that is preserved in the Geological Museum at Leiden. Von Koenigswald has afterwards visited these sites; the fossils are derived from the Poetjangan (Djetis) beds exclusively (Duyfjes, 1936, p. 138; Von Koenigswald, 1940, p. 47). The Cosijn collection in the Geological Museum at Leiden, most kindly entrusted to me by its director, Prof. Dr. I. M. van der Vlerk, is so important because it contains undoubted Djetis material that can be directly compared with undoubted Trinil material, viz., the specimens collected at the Trinil site by Dubois. At Trinil, Dubois's *Pithecanthropus* locality, fossils occur only in the Kaboeh (Trinil) beds; the underlying Poetjangan (Djetis) beds are unfossiliferous (Duyfjes, 1936, p. 146; Von Koenigswald, 1940, pp. 43, 51; 1950, p. 92). The specimens of *Epileptobos groeneveldtii* in the Dubois collection are from at least ten localities, among which Trinil (Coll. Dub. no. 2746). This specimen therefore proves that *Epileptobos* is not confined to the Djetis, but also occurs in the Trinil fauna.

In the Cosijn collection mentioned above there are horn cores and teeth indistinguishable from those of typical *Duboisia santeng* from Trinil in the Dubois collection. *Duboisia santeng* has to replace *"Antilope modjokertensis"* of Von Koenigswald as the material on which the latter is based is within the limits of the Trinil *Duboisia.* In the same way, *Bibos palaesondaicus* is not absent in the Djetis fauna as shown by horn cores in the Cosijn collection. *Bubalus* has already been recorded from the Djetis fauna by Von Koenigswald (1934, p. 193; 1935a, p. 193).

Consequently, the bovid faunas of the Djetis and the Trinil beds, to all intents and purposes, are the same, featuring two extinct and endemic genera, *Duboisia* and *Epileptobos,* as well as two modern genera, *Bibos* and *Bubalus* 1). The two last-mentioned genera occur in the Middle Pleistocene fauna

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1) However, a referred specimen of genus indet. (cf. *Antilope) saätensis* has been recorded from the Djetis beds; this form is not known from Trinil proper.

from Southern China (Colbert and Hooijer, 1953) with which the Djetis and Trinil faunas are clearly correlative (Hooijer, 1952, p. 442; 1954, p. 91/92; 1955, p. 5; 1956d, p. 7; 1957, p. 7).

Previous to his explorations in Java, Dubois collected subfossil mammalian material from limestone caves in Central Sumatra. The bovids of this portion of the Dubois collection, including *Capricornis* and *Bubalus* still living on the island as well as *Bibos,* the banteng now extinct in Sumatra, will be described in the present paper.

While searching for fossils in the Siwaliks of the Punjab in 1895 Dubois found two skulls of *Hemibos* first described in the present paper.

I am indebted to Dr. E. I. White, Keeper of the Department of Palaeontology of the British Museum (Natural History) at London, for giving me the opportunity to examine skulls of *Hemibos* and of *Leptobos* from the Upper Siwaliks. Mr. R. W. Hayman kindly sent me on loan a few skulls of *Tetracerus* preserved in the Mammal Department of the British Museum (Natural History). My thanks are due to Prof. Dr. I. M. van der Vlerk for permission to study material of *Duboisia, Epileptobos,* and *Bibos* from Djetis deposits of Java in the Geological Museum at Leiden.

All measurements in the present paper are in mm, unless otherwise stated. Skull measurements of the larger bovines are in 5 mm units; skull angles are taken in units of 5°.

Order ARTIODACTYLA Owen
Family BOVIDAE Gray
Subfamily BOVINAE Gill
Genus DUBOISIA Stremme
Duboisia santeng (Dubois) 1)

Anoa, spec. nov. Dubois, Natuurk. Tijdschr. Ned. Indië, vol. 51, 1891, p. 94.

Anoa santeng Dubois, in Jentink, Notes Leyden Museum, vol. 13, 1891, p. 221.

Duboisia santeng, Brongersma, Arch. Néerl. d. Zool., vol. 2, 1936, p. 247.

Tetraceros kroesenii Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 24, 1907, p. 454.

Tetracerus kroesenii Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1260.

Duboisia kroesenii, Stremme, in L. Selenka and M. Blanckenhorn, Die Pithecanthropus-Schichten auf Java, Leipzig, 1911, p. 115, pl. XVII figs. 12-14, pl. XIX figs. 3-5, pl. XX fig. 1; Von Koenigswald, De Ing. in Ned. Indië, vol. 1, sect. IV, 1934, p. 194, pl. III figs. 12-13; Wet. Med. Dienst Mijnb. Ned. Indië, no. 28, 1940, p. 61, pl. III figs. 2-3.

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1) A review of the early history of the name *Duboisia santeng,* which also includes references to the anonymous reports of the Dienst van het Mijnwezen (Mining Survey) published between 1891 and 1893, will be found in Brongersma (1936, pp. 246-247).

Antilope modjokertensis Von Koenigswald, De Ing. in Ned. Indië, vol. 1, sect. IV, 1934, p. 192, pl. III figs. 9-11; ibid., vol. 2, sect. IV, 1935, p. 87, pl. fig. 5; Wet. Med. Dienst Mijnb. Ned. Indië, no. 28, 1940, p. 62, pl. II figs. 3-4.

Antilope (*Duboisia*?) *modjokertensis* Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Indië, no. 28, 1940, p. 61.

Cervus spec. (pro parte), Stehn and Umbgrove, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 46, 1929, pl. IV fig. 3 (not figs. 1-2).

cf. *Antilope modjokertensis* (pro parte) Von Koenigswald, De Ing. in Ned. Indië, vol. 2, sect. IV, 1935, p. 87 (= *Cervus* spec., Stehn and Umbgrove, 1929, pl. IV fig. 3; not fig. 2).

The Trinil skull secured by the Selenka expedition has already been fully described and figured by Stremme (1911, pp. 115-124, pl. XIX figs. 3-5; pl. XX fig. 1). The Dubois collection contains a series of eighteen skulls (Coll. Dub. nos. 2037-2039, 2041-2051, 2071-2073, 2075) the majority of which with both horn cores in situ, as well as two entire frontals with horn cores (Coll. Dub. nos. 1666, 2040). In addition there are seventy-two isolated horn cores, some twenty-three of which are fit for measurement as the base is preserved. Adult male skulls of the nilgai, *Boselaphus tragocamelus* (Pallas), and of the four-horned antelope, *Tetracerus quadricornis* (Blainville), have been used for comparison since, as Stremme points out, it is to these forms that *Duboisia* is most closely related.

Stremme's description has brought out the main features of the present form. The skull described by him is more complete than any of the Dubois collection specimens in that at least one of the premaxillaries and both bullae are preserved, while the palate and the dentition are still attached to the skull although, as Stremme notes, the maxillary is displaced somewhat. In the *Duboisia* skulls collected by Dubois the muzzle is broken off; the skull base, if present, invariably lacks the bullae, and the maxillaries are detached from the skulls. One of the skulls of *Duboisia* (Coll. Dub. no. 2037, pl. I figs. 1, 3 and 8) possesses the posterior portion of the left zygomatic arch. The paramastoid process is entire in another skull (Coll. Dub. no. 2045). The zygomatic arches and paramastoid processes are broken off in the specimen that Stremme has described. The amount of individual variation disclosed by the Dubois collection series of skulls adds to our knowledge of the species in question. Therefore, a description of this material may be presented here.

There is also material of *Duboisia* in the Cosijn collection from the Djetis deposits North of Djetis and Perning, Eastern Java, preserved in the Geological Museum at Leiden. This material consists of horn cores as well as teeth, and will be recorded below. It is of certain interest as *Duboisia* has not been recorded before from the Djetis deposits. According to Von Koenigswald (1934, p. 198) *Duboisia* would be known with certainty from the Trinil deposits only, the Djetis deposits containing an antelope described by him as

Antilope modjokertensis "die *Duboisia* von Trinil an Grösse konstant etwas übertrifft. Da die Hörner noch nicht bekannt sind, vermag die Gattung noch nicht angegeben werden" (l.c., p. 192). As will follow from the present study *"Antilope modjokertensis"* is a synonym of *Duboisia santeng* (Dubois).

In table I are given the skull measurements of all the Dubois collection specimens of *Duboisia* as well as those of *Boselaphus* and *Tetracerus*. *Duboisia* is intermediate in skull size between the two Indian forms, and in its skull characters it is closer to *Boselaphus*, while in certain dental characters it is closer to *Tetracerus*.

The deep and well-marked lacrimal fossae found in *Tetracerus* do not occur either in *Duboisia* or in *Boselaphus*, and neither do the second pair of small horns that are often present just above the anterior edge of the orbit in *Tetracerus*. In *Duboisia* as well as in *Boselaphus* there are prominent precornual ridges on the frontals that converge to the front, although they do not actually meet in the median line. The skull surface between these ridges has a reticulate sculpture. The upper rim of the orbit is 2½-3 cm below the level of these ridges in *Duboisia*; in *Boselaphus* it is ½-1 cm below the level of the frontal ridges, and the orbit, therefore, is placed higher than that of *Duboisia*. In *Tetracerus* frontal ridges are hardly evident, and the orbit is high in position.

Just in front of the orbits the surface of the frontals is abruptly curved downward in *Duboisia* (pl. I fig. 9); the angle between the preorbital plane of the frontal and the fronto-parietal plane is 125-130°. In *Boselaphus* there is also a frontal bulge, but it is much less marked: the angle in question is only 170-175°. In *Duboisia* and in *Boselaphus* the surface of the frontal is almost flat anteroposteriorly above and behind the orbit, but concave transversely due to the prominence of the frontal ridges. In *Tetracerus* the frontal is slightly convex both ways.

Beyond the fronto-parietal suture, which is just behind the bases of the horn cores, the upper surface of the skull remains in the same plane as the frontal in *Duboisia* as well as in *Boselaphus*. In *Tetracerus* the frontal and parietal profile of the skull is slightly and gently rounded.

Two curved crests emerge at the posterior inner base of each of the horn cores and run backward over the parietal region (pl. I fig. 3). The shorter of these is slightly curved, with the convexity outward, and meets the corresponding crest of the other side in the median line almost 2 cm in front of the occipital crest. It is more marked and more irregularly formed than the longer parietal crest, which is curved with the convexity inward, does not meet its fellow in the median line, and runs out posteriorly into the lateral part of the occipital crest, forming the upper boundary of the temporal fossa.

The surface of the parietal is flat between the parietal crests, and convex laterally of these crests. There is very little individual variation in these characters in the series of *Duboisia* skulls. The configuration is essentially the same in *Boselaphus,* only the shorter parietal crest is more prominent, and the lateral convexity of the parietal is less marked. In *Tetracerus,* on the other hand, the shorter parietal crest is less marked than that in *Duboisia,* and the parietal is more convex laterally; the brain case is more swollen in *Tetracerus* than it is in the two larger forms.

The angle between the parietal and the supraoccipital, which forms a semicircular area on the upper surface of the skull just above the occipital crest in *Duboisia* as well as in *Boselaphus,* is 180° in the fossil form. The nilgai has the supraoccipital slightly convex anteroposteriorly, inclined to the parietal plane at angles of ca. 160°. In *Tetracerus* the supraoccipital is a raised area that follows the gentle curve of the fronto-parietal profile.

The angle between the parietal and the occipital planes (the plane of the occiput taken over the occipital crest and the upper border of the foramen magnum, in the median line) is 100-105° in *Duboisia,* much as in *Tetracerus* (ca.95-100°), whereas in *Boselaphus* this angle is only 70-80°. Hence, the occiput projects further backward above in *Boselaphus* than in *Duboisia,* or, the occipital condyles are much less prominent behind in *Boselaphus* than they are in the fossil form. This is a marked difference between *Boselaphus* and *Duboisia* not mentioned by Stremme, indicating that the poise of the head must have been different in the two forms. In *Duboisia* the head must have been carried more horizontally, less inclined downward than in *Boselaphus.* The strong downward bend of the preorbital skull profile in the fossil form as compared with the living is undoubtedly a difference likewise correlated with a different head poise, and so is the lower position of the orbit in *Duboisia* already noticed above. Unfortunately the lower margin of the orbit and the anterior zygomatic root are not preserved in any of the *Duboisia* skulls, but in one of them (Coll. Dub. no. 2037) the posterior portion of the zygomatic arch is in situ (pl. I fig. 1), and the portion is much more steeply inclined downward to the front than that in either *Boselaphus* or *Tetracerus.*

Coming now to the horn cores of *Duboisia,* there is a certain resemblance to those of the nilgai already noticed by Stremme. They are subtriangular at base and not very long, but rather markedly compressed from above downward: the anterior edge, which is a continuation of the frontal ridge, is much less prominent than that in *Boselaphus.* Whereas in the last the horn core is but slightly curved, and tapers very regularly toward the tip, in *Duboisia* the proximal half shows a slight taper only. The upward and forward curve of the horn core of *Duboisia* is more marked than that in *Boselaphus,* and the lateral edge is more convex throughout. There is very little resemblance with the cores in *Tetracerus,* which are almost devoid of keels, small, and only slightly divergent.

In *Duboisia* the horn cores project markedly sideways beyond the orbit; the maximum span of the horn cores exceeds the width at the posterior borders of the orbits (table I). In *Boselaphus* the span of the horn cores is less than the orbital width in three out of five adult skulls; in the remaining two the span of the horn cores exceeds the orbital width, although not to the extent seen in *Duboisia* (Coll. Dub. nos. 2038, 2046, 2049, and 2050). In the *Duboisia* skulls the cores are turned inward at the tip so that the interval between the tips is less than the maximum span of the cores; in the two *Boselaphus* skulls with rather divergent cores (Leiden Museum, cat. b and no. 9933) the maximum span of the cores is at their very tips. Two adult *Duboisia* skulls representing the extremes of variation in the span of the horn cores (Coll. Dub. nos. 2048 and 2049) are shown in frontal view on pl. I figs. 6 and 7.

The variation in size of the horn cores of *Duboisia* is considerable (table I), but this is partially due to age as the smallest entire horn core in situ (Coll. Dub. no. 2038) is of an immature individual; the sutures between the frontals and the parietals, and those of the supraoccipital are still open in this skull, whereas they are obliterated in the others.

Of the two horn cores in the Cosijn collection from the Djetis deposits preserved in the Geological Museum at Leiden, one (no. 27987) is a relatively large specimen, of the left side. It measures ca. 90 mm along the outer curve as far as preserved. Geol. Mus. Leiden no. 27904 is smaller (length 60 mm as preserved), with a basal transverse diameter of 30 mm; it is of the right side and most probably immature. These two specimens agree so perfectly with the *Duboisia* horn cores from Trinil as to leave no doubt that *Duboisia* formed part of the Djetis fauna as well as of the Trinil fauna. As already mentioned above, Von Koenigswald (1934, p. 198) believes *Duboisia* to be restricted to the Trinil beds.

The occiput of *Duboisia* is wider relative to its height than that in *Boselaphus* as shown by the occiput index in table I; it is entire only in four out of the eighteen skulls (Coll. Dub. nos. 2037, 2039, 2041, and 2045), and is characterized, as Stremme (1911, p. 116) notes, by the knob-like thickening above of the median vertical crest, on either side of which the surface is concave due to the prominence of the lateral occipital crests (pl. I fig. 8). The condyles are very prominent behind, and the paramastoid process (preserved on the left side in Coll. Dub. no. 2045; pl. I fig. 2) is slender and rod-like, not transversely compressed and plate-like as in *Boselaphus*. The bullae are missing in the Dubois collection specimens, but Stremme (l.c.) states that they project downward beyond the basioccipital, which is not the case in *Boselaphus* but which condition obtains in *Tetracerus*. In the development of the paramastoid process *Duboisia* is likewise closer to *Tetracerus* than to *Boselaphus*. On the other hand, the basioccipital has a marked median groove in *Duboisia* just as in *Boselaphus*; this groove does not show in *Tetracerus*.

All the skulls of *Duboisia* the measurements of which are given in table I originate from Trinil with the exception only of Coll. Dub. no. 2071, which is from Kebon Doeren. Of the horn cores the following are from localities other than Trinil: Coll. Dub. nos. 2060b, 6911, and 8894, Kebon Doeren; Coll. Dub. nos. 2052b and d, 2061g (a right and a left core), 2064b, 2069a, 2513, and 2516, Kedoeng Broeboes; Coll. Dub. no. 245, Pati Ajam; Coll. Dub. no. 2052a, Tegoean; Coll. Dub. no. 2040, Tritik. To this list of localities of *Duboisia* must be added: North of Djetis and Perning, for the two horn cores in the Cosijn collection mentioned above.

Both in *Boselaphus* and in *Tetracerus* the horns are restricted to males. The Dubois collection series of twenty skulls and frontals invariably show horn cores; there are no hornless specimens. If the females of *Duboisia* had been hornless one would have expected to find at least some hornless frontals among a series of twenty. Therefore, in my opinion there can be little or no doubt that *Duboisia* had horns in both sexes, which is one more character that sets it apart from the two living genera of Indian antelopes with which it has been compared above.

There are several mandibular rami of *Duboisia* in the Selenka collection but none of these is entire (Stremme, 1911, p. 120). Von Koenigswald (1934, pl. III figs. 10 and 12) figures two incomplete specimens, a portion of a right ramus with M_3 from Djetis, and a left horizontal ramus with P_2-M_3 from Trinil. The former specimen is referred to *"Antilope modjokertensis"*, the latter to *Duboisia kroesenii*. In the Dubois collection there are a great many rami of the mandible with teeth in situ. The teeth will be referred to in a later section. The mandible of *Duboisia santeng* resembles that of *Boselaphus tragocamelus* rather than that of *Tetracerus quadricornis* in the long anterior part of the ramus: the distance from the mental foramen to P_2 is twice the height of the bone half-way between, or more, in *Duboisia* and in *Boselaphus*, whereas in *Tetracerus* the length from the mental foramen to P_2 is only about one and one-half times the height in between. The ventral border of the horizontal ramus is rounded and slightly convex anteroposteriorly in the molar part, and becomes narrower and sharp behind the molars, as in the living species. Unfortunately the posterior margin of the vertical ramus as well as the condyle and the coronoid process are missing in the fossil specimens; in *Boselaphus* the vertical part is relatively wider and higher than that in *Tetracerus*. The mandible of *Duboisia* differs from both of these in the marked increase in height as we pass along the ramus from P_2 to M_3; in the fossil form the height of the ramus below the middle of M_3 is one and one-half times that below P_2 (both taken at the medial surface) as opposed to only about four-thirds in the living species. Two right mandibular rami of *Duboisia santeng* (Coll. Dub. nos. 2053 and 2068d, both from Trinil) are shown in pl. I figs. 4 and 5.

The dentition of *Duboisia*, as Stremme (1911, p. 120) has already pointed out, resembles that of *Boselaphus* in hypsodonty and in the presence of basal pillars; in the smoothness of the enamel and in the shape of the lower premolars *Duboisia* rather resembles *Tetracerus*. Actually, on close inspection, these resemblances do not appear to be very strong.

In the upper molars of *Boselaphus* the basal pillars are very slender (Schlosser, 1903, p. 167); they are similar in size to those in *Duboisia* the molars of which are only two-thirds as large as those of *Boselaphus*. Hence, the basal pillars are relatively stronger in the fossil than in the recent molars. On the other hand, in *Duboisia* basal pillars may be missing; there are a few upper molars of *Duboisia* in which there is no trace of a median pillar. In the lower molars of *Duboisia* the (external) basal pillars are not invariably present either. Not a single one out of the seven *Boselaphus* dentitions examined lacks the basal pillars.

The degree of hypsodonty of the *Duboisia* molars relative to that in those of *Boselaphus* is more difficult to make out, for such a comparison has to be made between unworn crowns of molars of the same serial position. Entire and unworn crowns are very rare among the fossil teeth. However, there is an almost unworn right M_1 of *Duboisia* in the Trinil collection (Coll. Dub. no. 2509a) that can be compared with the same molar, just touched by wear, in a young skull of *Boselaphus* in the Leiden Museum. As shown in table 1 the molar of *Duboisia* is higher-crowned than that of *Boselaphus*.

TABLE 1

Measurements of crowns of M_1 in *Duboisia* and *Boselaphus*

	Duboisia	*Boselaphus*
1. Transverse diam. at base	10	13
2. Greatest height (medial)	26.5	30
3. Ratio 1 : 2	0.38	0.43
4. Anteroposterior (medial)	15.5	21.5
5. Ratio 4 : 2	0.58	0.72

Stremme (1911, pp. 120 and 123) states that the lower premolars in *Tetracerus* and in *Duboisia* have outer folds, and are angular and wide behind, whereas those in *Boselaphus* are either flat or incurved laterally, and rounded and narrow behind. The difference is not very marked. The posterior outer fold in P_3 and in P_4 of *Boselaphus* is only weaker and less sharp than that in those of *Tetracerus* and in *Duboisia*, and hence the posterior outer rib of the premolars is less well marked off anteriorly, but the hinder end of the crown is as angular in *Boselaphus* as it is in *Tetracerus* and in *Duboisia*. Both in P_3 and in P_4 there are two anterior and two posterior wings, which soon coalesce upon wear, leaving only one anterior and one posterior wing on the crown surface even of slightly worn teeth. The inner cusp is strong and has a backward process that is united to the posterior inner wing basally, so that the posterior valley becomes closed inside, forming an isolated fossette in well worn teeth. This holds for *Duboisia* (see Stremme, 1911, pl. XVII fig. 14, P_3; in P_4 the posterior valley is still open internally) as well as for *Boselaphus* and *Tetracerus*. The premolars in *Duboisia* in all probability are more hypsodont than those in *Boselaphus*; an isolated and unworn P_4 sin. from Trinil (Coll. Dub. no. 2509b) has a crown height of 16.5 mm by an anteroposterior diameter of only 13.5 mm. Unworn crowns of the homologous tooth of *Boselaphus* are not available to me at present, however.

There is a slight difference in proportions of the lower premolar series not mentioned by Stremme: the anterior lower premolar, P_2, is more reduced relative to P_3 and P_4 in *Duboisia* than in *Boselaphus* and in *Tetracerus*. As can be seen from table 2, presenting the anteroposterior crown diameters of P_2 and $P_{3\text{-}4}$ as well as the length ratio $P_2 : P_{3\text{-}4}$, the front premolar P_2 in *Duboisia* is further on its way to reduction in length relative to $P_{3\text{-}4}$ (average 0.36) than that in *Boselaphus* (average 0.40) or in *Tetracerus* (one observation: 0.39).

Duboisia is further represented in the Dubois collection by large series of jaw fragments with teeth in situ as well as of isolated teeth. Most of these originate from Trinil, some from other localities (Kebon Doeren, Kedoeng Broeboes, Pati Ajam, Tegoean, all localities from which horn cores have also been obtained, above, p. 13), while a number of specimens are without a record for the exact locality. Next to this material I have also examined the teeth of *Duboisia* from the Poetjangan (Djetis) deposits North of Djetis and Perning, Eastern Java, part of the collection made by Cosijn (1931, 1932) and preserved in the Geological Museum at Leiden. In this area only Djetis and no Trinil fossils are found (Duyfjes, 1936, p. 138); the specimens are the following: part of a right mandibular ramus with M_1 (broken), $M_{2\text{-}3}$ (no. 27848), $M_{2\text{-}3}$ dext., associated (no. 27847), an M^3 sin., well preserved,

TABLE 2

Lower premolars of *Duboisia, Boselaphus,* and *Tetracerus*

	Length P_2	Length $P_{3\text{-}4}$	Length ratio $P_2 : P_{3\text{-}4}$
Duboisia (Trinil)			
Coll. Dub. no. 2053	8	20.5	0.39
Coll. Dub. no. 2065a	8.5	23	0.37
Coll. Dub. no. 2065b	7	20	0.35
Coll. Dub. no. 2067a	7.5	21.5	0.35
Coll. Dub. no. 2067b	8	23	0.35
Coll. Dub. no. 2068a	7.5	21	0.36
Coll. Dub. no. 2068c	7.5	22.5	0.33
Coll. Dub. no. 2068d	7.5	21.5	0.35
Boselaphus, Leiden Museum			
cat. ost. b, ♂	14	33.5	0.42
reg. no. 2319, ♂	12	31	0.39
reg. no. 9933, ♂	12.5	32.5	0.38
cat. ost. a, ♀	13	32	0.41
reg. no. 2147, ♀	13	33	0.39
Tetracerus, British Museum			
43.1.12.86, ♂	8	20.5	0.39

and another M^3 sin., much worn and damaged (no. 27815a). I have already referred to the two horn cores of *Duboisia* in the Cosijn collection. Finally, there is some material of *Duboisia* among the fossil molars from the Tjitaroem valley W. of Batoedjadjar, Western Java, that have been figured as *Cervus* spec. by Stehn and Umbgrove (1929, pl. IV figs. 1-3). In revising this identification, Von Koenigswald (1935b, p. 87) refers the specimens figured on pl. IV figs. 2-3 of Stehn and Umgrove (1929) to his *"Antilope modjokertensis"*, thereby considering the two figures to represent two views of one and the same lower molar that agrees in size with an M_2. However, on studying the teeth in question, which are now in the collection of the Geological Museum at Leiden (no. 28094), and comparing them with the figures presented by Stehn and Umbgrove, it became evident to me that pl. IV fig. 2 is the crown view of a lower molar of *Rusa,* and that pl. IV fig. 3 is an inner view of the unworn crown of a right M^3 of *Duboisia.* Its length is 17 mm, the anterior basal width, 15 mm, and the greatest height of the crown is 27 mm. There is nothing for it but to identify this molar as *Duboisia santeng*; it is within the variation limits of Trinil specimens of M^3 (table 3). The same holds true for the Djetis specimens in the Cosijn collection; there are no characters by which these teeth can be distinguished from their homologues in the Dubois collection series of specimens from Trinil proper (table 3).

It is Von Koenigswald's opinion that the antelope from the Djetis deposits is different from that of the Trinil deposits; this view is based on teeth, and

TABLE 3

Measurements of upper and lower last molars of *Duboisia* 1)

	M^3			M_3	
Coll. Dub. nos.	length	anterior basal width	Coll. Dub. nos.	length	basal width
1824a	17	15.5	1824f	21.5	10
1824b	18.5	17	1824g	24	12
1824c	19.5	17	1824h	22	10.5
1824d	20	17.5	1824i	25	11
1824e	18	16.5	1824j	24	11
2055	18.5	15.5	1824k	23	—
2056	18.5	15.5	1824l	19.5	10
2062a	17	—	2053	20	—
2062b	17	16	2057a	22	—
2062c	20.5	16	2057b	20	—
2062d	17	—	2062e	23	10.5
2063b	18	14.5	2063a	21	—
2066	17.5	—	2063c	21.5	—
2509c	18.5	16.5	2065a	21.5	—
2509d	17.5	16.5	2065b	19.5	—
2509e	17.5	16	2067b	21	—
2520a	17	—	2068a	20	—
2520b	17.5	—	2068b	21	—
8167a (Kedoeng Broeboes)	19	—	2068c	20	—
8167b (idem)	19.5	17	2068d	21.5	—
8167c (idem)	17.5	17	2509f	21.5	—
8167d (idem)	18	15	2509g	24.5	12
Cosijn coll. no. 27815a (Djetis)	17.5	17	2509h	19	10
			2510a	23.5	—
Stehn & Umbgrove no. 28094 (Batoedjadjar)	17	15	2510b	24	11.5
			2510c	23.5	10
			2510d	23	11
			2512a	19.5	—
			2517	21	—
			2520c	24	10.5
			2520d	23	10.5
			2520e	22	9.5
			2520f	24	11.5
			2520g	24	11
			2536	21.5	—
			2519 (Kebon Doeren)	21.5	10.5
			2576a (Tegoean)	21.5	10
			2515 (Pati Ajam)	20	9.5
			Cosijn coll. no. 27848 (Djetis)	24	—
			Cosijn coll. no. 27847 (Djetis)	—	12

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1) All specimens in this table are from Trinil, unless otherwise indicated.

not on horn cores, which have not been found by him in the Djetis deposits. The Djetis teeth are stated to be slightly larger in size than those of the Trinil *Duboisia* (Von Koenigswald, 1934, p. 192; 1940, p. 62). An unworn M_3 from Djetis is about 25 mm high by a length of 25 mm; in a mandible from Sangiran the length of M_3 is 24 mm (Von Koenigswald, l.c.). A left M_3 from the Tambakan deposits of Tjisaär, Western Java, equated to the Djetis deposits (Von Koenigswald, 1935b, p. 87, pl. fig. 5) is stated to be very typical of *"Antilope modjokertensis"*, agreeing fully with the Djetis types; it has a length of 23 mm. Table 3 shows that the length of M_3 in the Trinil *Duboisia* varies from 19 to 25 mm; this range also includes the Cosijn collection specimen already mentioned above. Therefore, the present study does not bear out the statement that the Djetis antelope "die *Duboisia* von Trinil an Grösse konstant etwas übertrifft" (Von Koenigswald, 1934, p. 192); although the Djetis specimens are to the higher side of the ranges of variation of their homologues from Trinil they are fully within these limits. The fact that two characteristic *Duboisia* horn cores have now been recorded from the Djetis beds (Cosijn collection) removes all doubt concerning the generic and specific identity of *"Antilope" modjokertensis*, which can now be placed in the synonymy of *Duboisia santeng* (Dubois).

There is another species of antelope in the Pleistocene of Java, which does not seem to be represented in the Dubois collection. It has been recorded from Kali Saät near Boemiajoe by Von Koenigswald (1934, p. 192, pl. III fig. 7) as *Antilope saätensis*. The right horizontal ramus of the mandible figured by Von Koenigswald, in which P_4 and M_3 are erupting and unworn, considerably exceeds in size those of *Duboisia santeng*; the alveolar length of the entire toothrow (P_2-M_3) of the Kali Saät specimen is given as 112 mm; in *Duboisia* this length varies from 73 to 84 mm only (table 4). Although there is always an appreciable amount of variation with wear and age in such overall length measurements because of decreasing length and increasing interproximal wear in the teeth of older individuals it does not seem likely that

TABLE 4

Alveolar length of lower tooth series in *Duboisia*

Coll. Dub. nos.	Length P_2-M_3	Coll. Dub. nos.	Length P_2-M_3
2053	74.5	2067b	84
2057a	82	2068a	75
2057b	78	2068b	ca. 79
2065a	81	2068c	80
2065b	73	2068d	79
		2512a	81

the size gap could be filled if more specimens had been available. Nevertheless, more material of *"Antilope" saätensis* is urgently needed, most of all the horn cores in the absence of which the generic determination must remain uncertain.

Genus EPILEPTOBOS Hooijer

Epileptobos groeneveldtii (Dubois)

Bos (of *Bison*?), spec. nov. Dubois, Natuurk. Tijdschr. Ned. Indië, vol. 51, 1891, p. 94.
Leptobos, Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 24, 1907, p. 454.
Leptobos groeneveldtii Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1261; Pilgrim, Mem. Geol. Surv. Ind., new series, vol. 26, 1939, pp. 303, 307, 308; Merla, Pal. Italica, vol. 46, 1949, p. 66.
Epileptobos groeneveldtii, Hooijer, Zool. Med. Museum Leiden, vol. 34, no. 17, 1956, p. 240.
Leptobos cosijni Von Koenigswald, De Ing. in Ned. Indië, vol. 1, sect. IV, 1934, p. 193, pl. III figs. 1-2; Wet. Med. Dienst Mijnb. Ned. Indië, no. 28, 1940, p. 62, pl. II fig. 2; Hooijer, Zool. Med. Mus. Leiden, vol. 34, no. 17, 1956, p. 240.
Bibos cosijni Von Koenigswald, De Ing. in Ned. Indië, vol. 1, sect. IV, 1934, p. 198.
Leptobos cf. *cosijni* Von Koenigswald, De Ing. in Ned. Indië, vol. 2, sect. IV, 1935, p. 87, pl. fig. 6.
L[eptobos] cosijni, Pilgrim, Mem. Geol. Surv. Ind., new series, vol. 26, 1939, pp. 302, 303.

Until now our knowledge of the present form was based on the brief diagnosis presented by Dubois (1908, p. 1261), on figures of the back part of a skull with portions of the horn cores from Djetis named *Leptobos cosijni* by Von Koenigswald (1934, pl. III figs. 1-2), and on some notes and measurements of one of the Dubois collection skulls (no. 2766) given by Pilgrim (1939, pp. 303, 307, and 308). My recent study of the entire Dubois collection material referable to this form has convinced me that the Java *"Leptobos"* is much more advanced than the species of *Leptobos* from the Villafranchian of India and Europe, a fact already noticed by Pilgrim (1938, p. 451; 1939, p. 307); for this reason I have raised it to distinct generic rank: *Epileptobos* (Hooijer, 1956 b). The study of the Dubois collection specimens shows that the difference in curvature of the horn core (more upward and less forward) that induced Von Koenigswald to regard his Djetis skull as specifically distinct from Dubois's *L. groeneveldtii* is of an individual nature only; as in fact has been noted by Von Koenigswald (1940, p. 62) in the Dubois collection there are skulls of the same type as that figured by him as *L. cosijni*. *Leptobos cosijni,* therefore, is a synonym of *Epileptobos groeneveldtii*. On the other hand, *Leptobos dependicornus* Dubois (1908, p. 1261/62), which Dubois considered to be probably the female of his *L. groeneveldtii* (l.c.), proved to be the female of *Bibos palaesondaicus* Dubois (this paper, p. 93).

The principal characters by which *Epileptobos groeneveldtii* (Dubois) is distinguished from *Leptobos* are as follows. Presence of horn cores not only in the males but also in the females. The horn cores themselves are larger, and shifted farther behind the orbits. The parietal is more reduced in size, and the interparietal is deflected fully into the plane of the occiput (as in *Bibos*). The occiput is triangular instead of semicircular, the upper angle in *Epileptobos* being formed by the parieto-occipital eminence, a feature not shown in *Leptobos*. The dentition of *Epileptobos* is as hypsodont as that in *Bibos*. Descriptions of thirty-eight skulls and parts of skulls are presented below.

The holotype of *Epileptobos groeneveldtii* (Dubois) is the back part of a skull from Wadegan (Coll. Dub. no. 2766, pl. II figs. 1-3) with both horn cores entire. The specimen is broken off obliquely in front: the right orbit is almost entirely gone but the posterior and upper surfaces of the left orbit are preserved as well as the squamosal part of the left zygomatic arch. The supraorbital groove is preserved on the left side only, the corresponding portion of the right frontal having broken away. It widens and flattens out toward the front.

At the broken edge of the left frontal, above the centre of the orbit, the supraorbital groove is less than 4 cm distant from the median line of the skull. It diverges backward from the median line, and the external orifice of the supraorbital canal, the supraorbital foramen, is 5 cm from the median line, at the level of the posterior edge of the orbit. Behind this point the supraorbital groove is roofed over by bone, but near its hinder end there is a small foramen, flush with the surface of the frontal, that is 7½ cm from the median line and 2½ cm behind the orbit. A similar foramen on the right side is only 5 cm from the median line, while it is placed slightly further back.

It is these two small foramina that have been mistaken by Pilgrim (1939, p. 307) for the true supraorbital foramina. Pilgrim writes that in "no. 2766, the supraorbital foramina are flush with the surface and not in pits", and further gives the distance between these supraorbital pits as 125 mm (l.c., p. 308). In reality, however, the small foramina in question are just accidental openings in or near the bony roof of the supraorbital grooves, such as occur in great variety in the banteng, in which they may form a chain of from two to six openings, never completely symmetrical on both sides of the skull. As seen on the left side of the present skull the supraorbital canal, however, opens into the deep groove, at the level of the posterior border of the orbit, at a distance of 5 cm from the median line. The orbital opening of the supraorbital canal is just below it, on a level with the posterior outer margin of the orbit. Of the right supraorbital canal part of the orbital opening only is preserved.

The frontals are slightly elevated in the median line between and behind the orbits, forming a weak sagittal crest; the surface of the frontals is concave transversely between the supraorbital grooves, and convex laterally of these grooves. The greatest width of the frontals, at the hinder edges of the orbits, must have been 240 mm; the least width, between the orbital margin and the base of the horn core, is 215 mm. The frontal surface is almost flat anteroposteriorly between the orbits, but becomes convex anteroposteriorly behind.

The horn cores are inserted a long way behind the orbits; the distance between the orbit and the base of the horn core (at the left side) is not less than 125 mm. At their bases the horn cores diverge posteriorly at an angle of 65°, and while curving outward and upward they decrease very gradually in diameters, the cross section remaining almost round throughout: 94 mm horizontally and 89 mm vertically at base; 74 by 70 mm at the middle of the length, and 39 by 35 mm at 7 cm from the tip. Only the basal third of the core is in the frontal plane; the cores gradually curve upward out of the plane of the frontals, and their tips are even slightly recurved forward. The length of the core from base to tip is 650 mm along the outer curve, and 480 mm across the chord of its curve. Each core describes just less than one-fourth of a circle. Their tips are 85 cm apart, and are elevated about 30 cm above the frontal plane. As shown by longitudinal grooves most developed along their posterior inner and front outer surfaces the cores are slightly twisted; the torsion is counter-clockwise for the right horn core, and amounts to one-fourth of a revolution.

The surface of the frontals between the horn core bases is concave transversely. On a level with the centres of the horn cores the surface of the skull is curved downward on the plane of the frontals at an angle of 145°. At the same level a sagittal crest emerges that gains in height and width posteriorly. The edge of this crest remains almost in the plane of the frontals in front of the cores, as do the basal parts of the horn cores, to the effect that two valleys are formed, diverging and rapidly deepening backward on either side of the sagittal crest, bounded laterally by the raised bases of the horn cores. The fronto-parietal suture is indistinct in the present specimen, but in others to be described later its two branches are seen to run along the bottoms of the two valleys between the median crest and the bases of the horn cores, joining in the median line just in front of the point of emergence of the sagittal crest, and indenting the frontals at approximately a right angle. The tip of the fronto-parietal suture is on a level with the centres of the horn cores. Thus, the sagittal crest is entirely on the parietal, and the plane of the fronto-parietal sutures is deflected out of the frontal plane at an angle of 145°.

The sagittal crest of the parietal expands posteriorly into a broad triangular eminence that is elevated 2½ cm above the surface of the fronto-parietal sutures. This is the most salient feature of the *Epileptobos* skull. The eminence, the parieto-occipital eminence, is only about 6 cm behind the point of emergence of the sagittal crest of the parietal, and it falls off steeply behind in the plane of the occiput. It has a median posterior projection that overhangs the occiput, extending 1 cm behind the lambdoid crest. The greatest basal width of the parieto-occipital eminence is 6½ cm; it merges laterally with the parietal crests that extend inward from the posterior inner bases of the horn cores, and which form the upper margins of the temporal fossae. The temporal fossae open on to the occiput just below the parieto-occipital eminence, and their hinder ends are 95 mm apart. When seen in occipital view, the parieto-occipital eminence forms the top of the occiput, which thereby assumes a triangular shape; the top of the parieto-occipital eminence is 3 cm above the level of the temporal contraction.

On the posterior surface of the parieto-occipital eminence, on either side of a short median crest extending downward from the median posterior projection, there is a small but deep depression. These two depressions are bounded below by the lambdoid crest, which is continuous with the temporal crests on either side that form the sides of the occiput. The temporal crests are very prominent behind, overhanging the whole of the occiput. The mastoid foramina form large, elongated pits. The external occipital protuberance, in the median line just below the lambdoid crest, is not very marked; it is flanked by two shallow depressions, much larger than the two depressions above the lambdoid crest already mentioned.

The plane of the occiput, taken over the lambdoid crest and the upper border of the foramen magnum, is inclined to the plane of the fronto-parietal sutures (the plane of the parietal, not counting the sagittal crest) at an angle of 115°. As the angle between the frontal and the parietal planes is 145° it follows that the frontal is inclined to the plane of the occiput at less than a right angle (80°).

The occiput is well preserved; measurements will be found in table 5.

The length of the temporal fossa, from the pterygoid crest to the temporal crest, is 155 mm; its height above the external acoustic meatus is 43 mm, and that above the glenoid cavity, 24 mm. The width of the brain case, at the middle of the temporal fossae, is 124 mm.

Coll. Dub. no. 2765 is a skull from Kedoeng Nojo (pl. III figs. 4, 6) with most of the maxillary and of the dentition but lacking the greater part of the right, and the tip of the left horn core.

TABLE 5

Measurements of the skull of *Epileptobos groeneveldtii*

Coll. Dub. nos.	2766	2765	2770	2829	2775	2767	2796	2786	2787	2789	2793	2794	2795
Median length of frontals	—	175	—	183	—	—	—	—	—	—	—	—	—
Median length of parietals	ca. 60	55	—	59	52	—	—	77	—	—	74	—	—
Distance from orbit to base of horn core	125	110	—	ca. 120	—	—	—	—	—	—	—	—	—
Width of frontals at orbits	240	—	—	—	—	—	—	—	—	—	—	—	—
Postorbital constriction	215	192	200	210	ca. 195	216	—	205	—	—	—	—	—
Diverging angle of horn cores	65°	70°	70°	65°	70°	65°	70°	—	—	—	—	—	—
Angle between frontal and parietal planes	145°	140°	145°	140°	140°	—	—	135°	—	135°	145°	—	—
Angle between parietal and occipital planes	115°	120°	115°	115°	120°	—	120°	115°	—	115°	110°	115°	110°
Temporal contraction	95	63	ca. 70	ca. 80	ca. 75	—	ca. 85	79	ca. 85	ca. 75	ca. 90	80	100
Greatest width of occiput	235	ca. 220	235	236	—	ca. 240	—	242	—	ca. 230	ca. 250	—	—
Width over paramastoid processes	170	168	170	ca. 170	ca. 170	176	—	170	164	ca. 165	173	—	—
Height from basion to top of eminence	156	160	—	170	—	167	—	176	—	160	157	—	157
From basion to lamboid crest	128	117	114	—	—	126	—	125	118	121	116	126	127
From upper border of foramen magnum to idem	95	83	79	—	ca. 85	85	ca. 95	89	81	82	ca. 80	91	91
Width of occipital condyles	110	103	107	ca. 100	—	103	—	112	109	100	—	107	108
Width of posterior tuberosities (basioccipital)	74	75	—	71	67	72	—	71	75	72	72	69	70
Width of anterior tuberosities of idem	39	39	38	34	—	34	—	42	35	39	39	33	41
Width of brain case at middle of temporal fossa	124	—	114	121	—	122	ca. 115	119	118	107	117	115	119

Little is left of the premaxillaries: only the posterior tips of their palatine processes and a small portion of the left nasal process are preserved. The nasals are missing for the most part, but the notch between the frontals into which fit their posterior extremities is distinct. The tip of the nasals is on a level with the anterior border of the orbit. The nasals indent the frontals at an angle of approximately 70°.

Part of the right nasal is present; it is slightly displaced but shows the presence of an ethmoidal vacuity at the point where it meets the lacrimal and the frontal, although the shape and size of this vacuity cannot be exactly determined.

The maxillaries, although their premaxillary and nasal margins are incomplete, are well preserved on the whole. The infraorbital foramina are placed above P^2 (broken off on both sides); the width over their inner borders is 93 mm. Above the junction of P^4 and M^1 are situated the facial tuberosities; the width of the muzzle over these tuberosities is 150 mm. A low ridge extends upward and backward from it to the anterior edge of the orbit.

The lacrimals are about 9 cm long, and narrow (height 2½ cm); the sutures between them and the frontals and jugals are not well shown.

The borders of both orbits are incomplete, especially anteriorly. The lower part of the orbital margin is very prominent laterally; the width of the skull over the lower borders of the orbits is 215 mm. At their narrowest part behind the orbits the frontals are 192 mm wide; the present skull, therefore, is narrower than that first described, which measures 240 mm over the orbits and 215 mm at the postorbital constriction.

The left orbit measures 62 mm in diameter vertically, and ca. 60 mm horizontally; it is filled with matrix.

The surface of the frontals is slightly elevated in the median line between and behind the orbits, and is almost flat anteroposteriorly. The supraorbital grooves are not roofed over by bone until a point 4 cm behind the orbits, at which level the distance between them is 12½ cm. The supraorbital foramina are situated just behind the posterior edge of the orbit, and are 11 cm apart; the right foramen is placed a little further back than that on the left side. In front of the supraorbital foramina the grooves converge still further, but they flatten out within a few cm of length.

The horn cores diverge posteriorly at a very slightly wider angle than do those in Coll. Dub. no. 2766; the angle of divergence is 70°. The distance between the orbit and the base of the horn core is slightly less, 110 mm. The basal diameters of the cores are 102 mm horizontally and 86 mm vertically. The right core is broken off at 12 cm above its base, but the left has a length along its outer curve of 660 mm as far as preserved; the apical portion is missing. The diameters at the middle of the length are 80 by 63 mm, and the broken end surface measures 52 by 38 mm. Thus, the core is more compressed than those of the preceding specimen. As in that specimen, however, the basal third remains in the plane of the frontals. The upward curve is less, the outward and forward curve are more marked than in Coll. Dub. no. 2766; in the present specimen the left horn core describes just about one-half of a circle, with a radius of 20 cm, and the (broken) tip is elevated 25 cm above the plane of the frontals. Some longitudinal grooves are seen to run along the posterior inner surface, but these do not extend to the apical portion and do not give any evidence of torsion.

The surface of the frontals, which is approximately flat anteroposteriorly over most of its length, becomes convex between the bases of the horn cores. At this level the frontals are indented by the parietals at an angle of 75°; the sutures are visible. The plane of the fronto-parietal sutures is deflected out of the frontal plane at an angle of 140°, and just behind the median tip of the fronto-parietal suture there emerges a sharp sagittal crest that increases in height posteriorly as much as the plane of the fronto-parietal sutures loses in height, to the effect that the edge of the sagittal crest of the parietal remains in the plane of the frontal. The sagittal crest widens behind into the parieto-occipital eminence that forms the top of the occiput. The total length of the parietal from the anterior point of the fronto-parietal suture to the hinder surface of the parieto-occipital eminence is 55 mm; less than one-third the median length of the frontal bones (175 mm). The greatest height of the eminence above the plane of the fronto-parietal sutures is 3 cm, and its basal width is 4½ cm. As in the preceding specimen, the parieto-occipital eminence has a median posterior projection that extends 1 cm behind the lambdoid crest. The two depressions below this posterior projection are very small; they are on a level with the temporal contraction, which is only 63 mm.

The temporal crests are as prominent posteriorly as those in the preceding specimen. The plane of the occiput, over the lambdoid crest and the upper border of the foramen magnum, is inclined to the parietal plane (not counting the sagittal crest) at an angle of 120°, which gives the same angle between the frontal and the occipital planes as that in Coll. Dub. no. 2766, viz., 80°.

The width and height measurements of the occiput of the present specimen do not differ much from those of Coll. Dub. no. 2766 (table 5). On the basal surface of the skull, the posterior tuberosities of the basioccipital are even more prominent relatively than those in the preceding specimen. The bulla ossea is almost entire on both sides; it does hardly project downward beyond the median level of the basioccipital, and is much compressed laterally. The left temporal fossa is filled with matrix, which has saved the zygomatic arch;

the height of the temporal fossa is 38 mm above the external acoustic meatus, and 18 mm above the glenoid cavity.

The palate and most of the dentition are excellently preserved in the present specimen; only the right and left P^2 and the right P^3 have broken off. M^3 extends backward to just behind the lateral post-palatal notches. In the median line the palate extends backward to 1½ cm behind the level of the posterior edges of M^3; it is not united to the vomer. The anterior palatine foramina are on a level with the back halves of M^2. The palate is slightly concave transversely between the teeth; it narrows and becomes markedly concave just in front of the premolars. The width of the palate between the molars is 84 mm.

The premolars and molars of the present skull appear to be indistinguishable in shape and size from those of the living female banteng (*Bibos javanicus*); I have carefully compared the development of the styles, accessory inner columns, shape of the fossettes, and degree of hypsodonty, and can find no constant character by which the fossil molars can be differentiated from recent female banteng molars in a corresponding stage of wear. As far as size and degree of hypsodonty are concerned this is borne out by table 6, in which are given the measurements of the teeth of two *Epileptobos* skulls (Coll. Dub. nos. 2765 and 2829), and those of two female banteng skulls

TABLE 6

Measurements of upper teeth of *Bibos javanicus* and of *Epileptobos groeneveldtii*

	Bibos reg. no. 15400	*Epilcptobos* Coll. Dub. no. 2765	*Bibos* cat. c	*Epileptobos* Coll. Dub. no. 2829
P^3, anteroposterior	18	19	—	—
transverse (top)	14	14	—	—
idem (alveolus)	16	17	—	—
P^4, anteroposterior	15	15	—	16
transverse (top)	16	15	—	19
idem (alveolus)	19	19	—	20
M^1, anteroposterior	22	24	22	22
transverse (top)	17	18	20	21
idem (alveolus)	21	22	23	23
M^2, anteroposterior	25	27	26	26
transverse (top)	17	18	20	21
idem (alveolus)	20	22	23	23
M^3, anteroposterior	27	28	29	30
transverse (top)	18	18	20	21
idem (alveolus)	20	21	22	24
Length P^2-P^4	53	55	58	—
Length M^1-M^3	74	78	78	80

(Leiden Museum, reg. no. 15400, and cat. ost. c) in corresponding stages of wear.

It will be observed that in the recent banteng we find the same differences in transverse diameter of the molar crowns at the top and at the alveolar margin that we find in *Epileptobos*; hence, there does not appear to be a difference in degree of hypsodonty between the fossil genus and the recent banteng. Neither is there a difference in the relative length of the premolar series between the two forms.

As the maxillary-palatine suture is visible in Coll. Dub. no. 2765 it is possible to measure the median length of the maxillary, which is just 100 mm. The median length of the palatine is 78 mm. The combined lengths of maxillary and palatine just exceed the length from basion to the lateral postpalatal notches, which is 175 mm.

The height of skull Coll. Dub. no. 2765 from the palatines to the tip of the naso-frontal suture is 130 mm.

The difference between the two skulls of *Epileptobos* thus far described is mainly in the curvature and the amount of flattening of the horn cores. While in both the angle of divergence of the cores at base is about the same (65-70°), and the basal third of the core remains in the frontal plane, the amount of curvature is less in Coll. Dub. no. 2766, in which the outer surface describes about one-fourth of a circle with a radius of ca. 35 cm, while in Coll. Dub. no. 2765 the radius of outer curvature of the core is only 20 cm. In the latter skull, the forward curve of the apical portion of the horn core is stronger than that in the former: a projection of the tip of the core on the plane of the frontal is about 15 cm in front of the occipital level in Coll. Dub. no. 2765, whereas in Coll. Dub. no. 2766 the projection of the tip of the core is about the same distance behind the occiput. The vertical flattening of the horn core is more marked in Coll. Dub. no. 2765 than in Coll. Dub. no. 2766, as can be seen from the measurements given. Added to that, the torsion of the horn core in Coll. Dub. no. 2766 cannot be observed in Coll. Dub. no. 2765.

It is therefore, interesting to find that other skulls of *Epileptobos* in the Dubois collection are intermediate between the two just described in all these characters of the horn cores, which tends to show that these differences are of an individual nature only. Such an intermediate specimen is Coll. Dub. no. 2770, from Tritik. It represents only the back part of a skull, broken off at the postorbital constriction, and, therefore, lacking the orbits. The right horn core is broken off above the end of the temporal fossa, and the parieto-occipital eminence is missing. The left horn core, however, is complete except for its tip.

The frontals of Coll. Dub. no. 2770 are shaped as in the preceding specimens, with a weak sagittal crest, almost flat anteroposteriorly in front of the base of the horn cores, and concave transversely between the bases of the cores. The posterior end of the supraorbital groove is seen only on the right side, extending just behind the narrowest part of the frontals, which measure 200 mm transversely (215 mm in Coll. Dub. no. 2766; 192 mm in Coll. Dub. no. 2765).

The base of the left horn core of Coll. Dub. no. 2770 diverges backward at an angle of 35° from the median line; the angle of divergence of the cores, therefore, was 70°. The core measures 95 mm horizontally, and 86 mm vertically at base. The curvature is more outward and less upward than that in Coll. Dub. no. 2766, but less outward and more upward than that in Coll. Dub. no. 2765; the basal third remains in the frontal plane.

The length of the core from base to broken end is 590 mm along the outer curve, and 360 mm in a straight line, as a chord to its curve. If, for comparison, we set out a portion of 590 mm from the base along the more complete cores of Coll. Dub. nos. 2766 and 2765 we find that the lengths of these portions across the chord of their curves are 440 mm in the former, and 270 mm in the latter, which shows that the core of Coll. Dub. no. 2770 is perfectly intermediate in amount of curvature between those of the two first described.

The diameters of the core of Coll. Dub. no. 2770 are 80 by 71 mm at the middle of the length; the broken end is about 40 mm in diameter. The outer surface of the core as far as preserved describes slightly over one-fourth of a circle, with a radius of 25 cm, intermediate between those found for Coll. Dub. no. 2766 (ca. 35 cm) and Coll. Dub. no. 2765 (20 cm). The amount of forward curvature is also intermediate, for a projection on the frontal plane of the end of the core of Coll. Dub. no. 2770 is about at the occiput. The diameters given indicate that the core of the present specimen is more compressed vertically than that of Coll. Dub. no. 2766, but less so than that in Coll. Dub. no. 2765. There is some evidence of clockwise torsion in the left horn core of Coll. Dub. no. 2770, not quite one-fourth of a revolution over the length of the preserved portion; the torsion, therefore, was counterclockwise in the right horn core, as in Coll. Dub. no. 2766.

Only the anterior part of the sagittal crest of the parietal is preserved in Coll. Dub. no. 2770; the inclination of the parietal plane on either side of it to the plane of the frontal is 145°, as in the holotype. The parieto-occipital eminence cannot be studied in the present specimen, but the angle between the parietal plane and that of the occiput (over the lambdoid crest and the upper border of the foramen magnum) is 115°, again as in Coll. Dub. no.

2766. The least width of the occiput between the ends of the temporal fossae is ca. 70 mm by a width of the brain case (at the middle of the temporal fossae) of 114 mm, less than that in the holotype (124 mm), although the greatest width of the occiput is the same in both, viz., 235 mm. Further skull measurements will be found in table 5.

Coll. Dub. no. 2829 (loc. ?) is a skull without the premaxillaries, the nasals, and the anterior portions of the maxillaries, but with the right P^4-M^3 and the left M^{1-3}, which have already been dealt with above in connexion with the dentition of Coll. Dub. no. 2765. The lateral surfaces of the maxillaries are damaged, and the frontal is crushed in front of the left orbit. The notch between the frontals for the posterior ends of the nasals is indistinctly seen. The jugals are missing on both sides, and the upper and posterior borders of the left orbit as well. Good portions of both horn cores are preserved, however.

Of the supraorbital canal both the external and the orbital openings are visible on the right side; the canal is on a level with the posterior border of the orbit. The supraorbital foramen is at a distance of 6 cm from the median line, and situated in a groove that converges to the median line in front and flattens out already above the orbit.

The distance between the posterior border of the orbit and the base of the horn core (at the right side) is ca. 120 mm; the frontal surface is shaped as in the preceding specimens, and the postorbital constriction is 210 mm.

The bases of the horn cores diverge backward at an angle of 65°, their basal diameters are 86 mm horizontally and 82 mm vertically. The preserved portion of the right core has a length of 20 cm along the outer curve (broken end ca. 65 mm in diameter), that of the left horn core measures 37 cm along the outer curve (diameter at broken end ca. 52 mm), of which the basal half remains in the plane of the frontals. Although it is more slender everywhere, in its outward and upward curve the core of Coll. Dub. no. 2829 resembles that of Coll. Dub. no. 2770 very closely. The amount of curvature is also much the same: a portion of 37 cm from the base along outer curve measures 25 cm across the chord of its curve in Coll. Dub. no. 2770 against 24 cm in Coll. Dub. no. 2829. The length of the basal 37 cm, across the chord of the curve, is 30 cm in Coll. Dub. no. 2766, and 22 cm in Coll. no. 2765. Therefore, the present specimen (Coll. Dub. no. 2829), just as Coll. Dub. no. 2770, is intermediate in horn core curvature between the two specimens first described.

The plane of the fronto-parietal sutures is inclined to the frontal plane at an angle of 140°. The parietals indent the frontals at an angle of ca. 85°, and on the parietals begins the sagittal crest that rises to a height of 3 cm above the plane of their sutures with the frontals. The length of the parietals (59 mm) is less than one-third that of the frontals (183 mm). The parieto-occipital eminence, with a basal width of 5½ cm, has a median posterior prominence extending almost 1½ cm behind the lambdoid crest. The depressions on either side of this prominence, just above the lambdoid crest, are so small as to be almost absent.

The occiput, of which the right condyle is missing and the upper border of the foramen magnum damaged, forms an angle with the parietal plane of 115°. The skull base is very imperfect, but the tuberosities on the basioccipital are preserved. The palate extends 1 cm behind M^3 in the median line, and the last molars extend slightly less than 1 cm behind the lateral postpalatal notches. The length from these notches to the basion is 167 mm (175 mm in Coll. Dub. no. 2765).

The palate is slightly wider between the inner surfaces of M^1 (86 mm) than between those of M^3 (80 mm); in Coll. Dub. no. 2765 these widths are the same (84 mm). The premolars and molars are indistinguishable from those of the modern female banteng, as already stated above (p. 26).

The height of the skull from the palatines to the tip of the nasofrontal suture is ca. 135 mm (130 mm in Coll. Dub. no. 2765).

Coll. Dub. no. 2775, from Tritik, is the back part of a skull broken off at the orbits. The right horn core is preserved for a length of 37 cm from the base along the outer curve, while the left is 16 cm long; the diverging angle of the cores is 70°. The basal diameters are 97 mm horizontally and 84 mm vertically. About one-half of the preserved portion of the right core is in the frontal plane, and its straight length across the chord of the curve is 24 cm, whereby it agrees closely in degree of curvature with the cores of Coll. Dub. nos. 2770 and 2829. The diameters at two-thirds of its length from the base are 83 mm horizontally and 71 mm vertically; hence the compression is very nearly the same as that of the core of Coll. Dub. no. 2770. The longitudinal grooves are not very marked, and indicate a slight counter-clockwise torsion of the right horn core, just as in Coll. Dub. no. 2829.

The fronto-parietal suture indents the frontals at an angle of almost 90°. The median tip of the suture is opposite the centres of the horn cores, and its plane is inclined to that of the frontals at an angle of 140°, as usual. The parietal is very short: the length from the median tip of the fronto-parietal suture to the hinder surface of the parieto-occipital eminence is 52 mm; unfortunately the median length of the frontals cannot be determined as the naso-frontal notch is not shown. The sagittal crest of the parietal, however short, is steep and high; the height of the parieto-occipital is 3½ cm above the plane of the fronto-parietal sutures. The posterior prominence, however, is almost nil; the hinder surface of the parieto-occipital eminence is fully in the plane of the occiput. Depression at its base posteriorly, above the lambdoid crest, cannot be distinguished. The angle between the parietal plane (not counting the sagittal crest or the eminence) and that of the occiput is 120°.

The parietal and temporal crests are rather damaged in the present specimen, and the occipital condyles are gone. Such measurements as can be given will be found in table 5.

Coll. Dub. no. 2767, a skull from Kedoeng Pingit with the greater parts of both horn cores, is broken off at the orbits. The surface of the frontals in front of the postorbital constriction (which is 216 mm) is crushed; the frontal plane, therefore, cannot be exactly determined. The horn cores, diverging posteriorly at an angle of 65°, measure 99 mm horizontally and 87 mm vertically in diameters at base. They are remarkable for their curvature, which is stronger than that in any of the previously described specimens. The radius of the outer curve of the right horn core is 18 cm, less even than that of the core of Coll. Dub. no. 2765, which it resembles closely in its outward and apically forward curve. The length of the right core of Coll. Dub. no. 2767 is 49 cm along the outer curve from the base to the broken end (diameters 68 by 57 mm). The length of the left horn core is 38 cm as preserved; its broken end surface measures 79 by 62 mm. There is a slight torsion, counterclockwise in the right horn core.

The present skull is wider at the frontals as well as at the occiput (table 5) than is Coll. Dub. no. 2766 with its slightly curved horn cores (radius of outer curve ca. 35 cm); at the same time it has its cores more strongly curved than those in the narrowest skull Coll. Dub. no. 2765, which shows that there is no correlation between the width of the skull and the degree of curvature of the horn cores in *Epileptobos.*

The state of preservation of the parietals on either side of the sagittal crest does not permit to determine the plane of the fronto-parietal sutures, or the height of the parieto-occipital eminence. The latter has a backward projection of 1 cm beyond the lambdoid crest, as usual. The depressions on either side of the median line just above the lambdoid crest are distinct in this specimen.

Coll. Dub. no. 2796 (loc. ?) is a skull fragment with most of the right horn core; the left is preserved only to above the posterior end of the temporal fossa. The frontals are broken off behind the orbits. The diverging angle of the horn cores is 70°. The length of the right core is 45 cm along the curve; the length of a portion of 37 cm is 25 cm across the chord of its curve, which shows it to be a moderately curved specimen such as those of Coll. Dub. nos. 2770, 2829, and 2775. The diameters at base (83 mm horizontally, 76 mm vertically) indicate that it is about as slender as the cores of Coll. Dub. no. 2829. The torsion is slight, and counter-clockwise.

The suture between the frontals and the parietals is indistinct, and the parieto-occipital eminence is incomplete. The angle between the parietal and the occipital planes can be measured, and is 120°. The borders of the occiput and the base of the skull are too much damaged for the usual measurements to be taken.

Coll. Dub. nos. 2833 and 2980 are right and left frontal portions with horn cores from Tegoean, which fit along a portion of the sagittal suture. Although the skull is not extraordinarily wide (postorbital constriction 210 mm) it has horn cores of truly gigantic proportions, which diverge posteriorly at an angle of 70°. The right horn core is entire, and has a length of 89 cm along the outer curve. The basal diameters are 111 mm horizontally and 82 mm vertically; diameters that have diminished only to 84 mm and 68 mm, respectively, at the middle of the length. Apically the cross section becomes almost round, 34 by 31 mm at 7 cm from the tip. The curvature is backward and outward, then upward, forward, and finally inward. At two-thirds of the length of the core from the base the outer surface is at its greatest distance from the sagittal plane of the skull, 45 cm. The left horn core resembles the right closely, and has a length of 70 cm along the curve as far as preserved. The maximum span of the horn cores (at two-thirds of their length from the base) is 90 cm. The tip of the entire right horn core projects inward, and is only 22 cm distant from the sagittal plane of the skull. It is elevated about 35 cm above the frontal plane. The tips of the horn cores, therefore, would have been only 44 cm apart.

Unfortunately nothing of the parietals or of the occiput is preserved in the present specimen. Its horn cores are by far the largest in the Dubois collection. The longest complete cores above described, those of the holotype Coll. Dub. no. 2766, measure 650 mm along the curve. Their maximum span is 85 cm, between the tips, as the tips are not turned inward in this specimen. Their elevation above the frontal plane is about the same (30 cm), however. The maximum span of the horn cores of Coll. Dub. no. 2765 would have been 76 cm, as the outer surface of the preserved left core is at most 38 cm from the sagittal plane of the skull. The apical portion is turned inward, but is incomplete, and the distance between the tips, therefore, unknown.

The amount of vertical compression of the cores at base is greater in the

Tegoean skull fragment (Coll. Dub. nos. 2833 and 2980) than that in any other specimen; yet the cores agree with the other *Epileptobos* specimens in their diverging angle (70°) as well as in the slight counter-clockwise torsion of the right core, which is one-fourth of a revolution as shown by longitudinal grooves along the upper and posterior surfaces.

One isolated but complete horn core remains to be described. It is of the left side, and originates from Tegoean (Coll. Dub. no. 2622). The length along the outer curve is 75 cm, whereby it is the second longest complete *Epileptobos* horn core in the collection. The diameters are 88 by 79 mm at base, 70 by 54 mm at the middle of the length, and 31 by 28 mm at a distance of 7 cm from the tip. Longitudinal grooves indicate a torsion, clockwise (left core!), of one-fourth of a revolution along the entire length. The radius of outer curvature is ca. 35 cm, as is that of cores of Coll. Dub. no. 2766; only the present specimen is longer. Too little of the adjacent portion of the frontal is preserved to determine the position of the core relative to the frontal plane or the diverging angle of the horn cores.

One isolated and incomplete horn core deserves special attention as it originates from Trinil. At this locality *Epileptobos* must have been scarce, as the present specimen (Coll. Dub. no. 2746) is the only horn core of *Epileptobos* from Trinil in the Dubois collection. It is of the right side, and the base of the horn core proper is perfect. The length, along the outer curve, is 52 cm to the broken end. The basal diameters are 97 mm horizontally, and 84 mm vertically; those at the middle of the length are 87 and 70 mm, respectively, while at the broken end the core still measures 55 by 45 mm in cross section. In amount of curvature the present specimen (Coll. Dub. no. 2746) resembles the cores of Coll. Dub. nos. 2770, 2829, and 2775 closely: the length of the basal 37 cm, measured across the chord of its curve, is 25 cm. The torsion of the horn core is counter-clockwise as indicated by heavy longitudinal grooves along the posterior surface.

Further specimens of isolated and incomplete horn cores are of no avail because of their bad state of preservation, which does not permit of accurate measurement. There remain, however, a great number of skull fragments, some of which with part of the horn core above the pedicle preserved. These specimens will be considered on the following pages.

Coll. Dub. no. 2786, from Kebon Doeren, is a portion of a skull with the horn cores broken off at base (pl. III fig. 5, pl. IV fig. 3). The left side of the skull, more complete than the right, is broken off at the level of the posterior margin of the orbit, with the supraorbital canal just preserved at the broken edge, 5½ cm from the median line. At the right side the orbit is entirely gone, and so is the lateral surface of the frontal between the orbit and the horn core. The zygomatic arches are missing.

The frontals are slightly convex anteroposteriorly and concave transversely between the horn core bases. The fronto-parietal suture is very clearly shown. The two branches indent the frontals at about a right angle, opposite the centres of the horn cores, and run outward and backward along the bottoms of the valleys between the sagittal crest of the parietal and the raised horn core bases. They are situated in a plane that is inclined to the frontal plane at an angle of 135°. The sagittal crest of the parietal is well developed; it emerges just behind the median point of the fronto-parietal suture, is convex throughout, and rises to a height of 4 cm above the sutures on either side. It gradually widens backward until, just above the lambdoid crest, it has a basal width of 6 cm. The posterior surface of the parieto-occipital eminence thus formed is in the plane of the occiput. The median length of the parietal, to the posterior surface of the parieto-occipital eminence, is almost 8 cm (77 mm). The eminence has a basal median projection that extends 1½ cm beyond the lambdoid crest.

On the posterior surface of the eminence, about 2 cm above the median basal projection, there is a small foramen. Each of the two depressions below the median projection, just above the lambdoid crest, also has a foramen. These small openings, the presence of which could not be ascertained in the skulls already described above but which will be noticed in several specimens to be described further on, are evidently for the outlet of vessels. As similar foramina are found in *Leptobos* and in *Bibos* it is of importance to note their presence in *Epileptobos*. In the present specimen (Coll. Dub. no. 2786) the two basal foramina are 16 mm apart, and are 32 mm below the upper central foramen on the posterior surface of the parieto-occipital eminence.

The parietal crests are short, only 5 cm from their point of emergence at the postero-internal side of the horn core base to the hinder end of the temporal fossa, and rather prominent. One branch of each continues inward beyond the hinder end of the temporal fossa, toward the median line, forming together the base of the posterior surface of the parieto-occipital eminence; the other curves sharply downward and outward at the end of the fossa, and is continuous with the temporal crest that forms the hinder margin of the temporal fossa, overhanging the occiput. The hinder ends of the temporal fossae are 79 mm apart, but the least width of the occiput at this level is 87 mm due to the prominence of the crests bordering the fossae.

The sutures of the parietal are also clearly shown in the temporal fossa;

in the skulls thus far described these sutures are indistinct. The present specimen, however, as well as several others to be noted below, show how the parietal enters into the formation of the temporal fossa. The parietal forms a tongue along the upper part of the temporal fossa that extends over most of the length of the fossa, just as in *Bibos.* The length of the temporal fossa, from its hinder end to the pterygoid crest, is 150 mm, and the parietal extends forward to only 35 mm from the pterygoid crest, that is, over almost four-fifths the length of the temporal fossa. The height of the temporal fossa is 50 mm above the external acoustic meatus.

The occiput is well preserved except for the paramastoid processes, which are almost entirely missing. The angle between parietal and occiput planes is 115°. The external occipital protuberance, in the median line just below the lambdoid crest, is only slightly developed, as in the other specimes. The two depressions flanking it are shallow but extensive. The mastoid foramina are more open than in any of the specimens described above. Skull measurements given in table 5 show that the occiput is wider than that in any specimen thus far described, while in height it also exceeds the others, which is, however, due to the prominence of the parieto-ocipital eminence as the height from the basion or from the upper border of the foramen magnum to the lambdoid crest is not greater than in some of the others.

Coll. Dub. no. 2787 (Tegoean) is a skull portion without the orbits, while in addition to the horn cores the parieto-occipital eminence has broken away. Of the frontal surface enough is preserved in the median line to determine the frontal plane. As the part of the occiput missing is only that above the lambdoid crest it is possible to measure the angle between frontal and occiput planes, which is 70°, just as in the preceding specimen. The temporal fossae are well shown on either side, and the parietal is seen to extend forward to a point ca. 35 mm behind the pterygoid crest, by a length of the temporal fossa of over 140 mm(hinder ends damaged). Most of the measurements of the occiput can be given (table 5).

Coll. Dub. no. 2789, from Kedoeng Broeboes, a fronto-occipital skull portion with the horn cores broken off at base, is somewhat corroded but has most of the parieto-occipital eminence. The median foramen on its posterior surface, 2½ cm above the posterior basal projection, is well shown; the foramina in the depressions on either side of the median line just above the lambdoid crest, however, do not show. The angle between the parietal and the frontal planes is 135°, that between the parietal and the occiput is 115°, which gives an angle between the frontal plane and that of the occiput of 70°, as in the two preceding specimens. The parietal extends forward in the temporal fossa even further than in the other skulls: the length of the fossa is 130 mm from its hinder end to the pterygoid crest, and the parietal has a length of 115 mm, ending only 15 mm behind the pterygoid crest. The skull is rather narrow at the brain case and the condyles (table 5).

Coll. Dub. no. 2793 is a fronto-occipital portion from Kedoeng Broeboes, again with the cores broken off at their bases, in which the parietal sutures are fairly distinct. The length of the parietal, in the median line, is 74 mm. However, there is no trace of a sagittal crest on the parietal leading upward into the parieto-occipital eminence in this specimen: the parietals are hardly raised in the median line until a point 4 cm behind their median anterior point, where they are sharply curved upward to form a strong parieto-occipital eminence that is elevated 2½ cm above the plane of the fronto-parietal sutures. The basal width of the eminence is 7½ cm, and there is a median foramen posteriorly near the top, 2½ cm above the posterior projection that overhangs the lambdoid crest. The eminence is damaged on the left side, but in the depression on the right side, above the lambdoid crest, there is a foramen, only 7 mm from the median line.

The angle between the frontal and the parietal planes is more open than that in most of the other skulls, 145°, as it is in Coll. Dub. nos. 2766 and 2770 too. The angle between the parietal plane and that of the occiput, 110°, is less than that in any other specimen (115°-120°). The left occipital condyle is missing, and the temporal crest is much damaged on the left side. The right temporal crest and hinder end of the temporal fossa, however, are well preserved: the length of the fossa is 152 mm, and the length of the parietal extending forward along its upper part is 132 mm. In width across the tubercles above the external acoustic meatus the occiput exceeds all the other specimens.

In none of the remaining skull portions of *Epileptobos* enough of the frontals is preserved to determine the frontal plane, and, further, the angle between the parietal and the frontal planes. Two specimens have at least the occiput well preserved; these are Coll. Dub. nos. 2794 and 2795. In both the horn cores are broken off at their bases; in Coll. Dub. no. 2794 (Tritik) the pterygoid crests are missing so that the length of the temporal fossa cannot be given. The parieto-occipital eminence is rather incomplete, but the sagittal crest of the parietal is as distinct as in the other specimens (Coll. Dub. no. 2793 excepted). The angle between the parietal plane and that of the occiput is 115°. Even though the posterior surface of the parieto-occipital eminence is damaged, the median foramen near the top is shown; it is 3½ cm above the lambdoid crest. In the temporal fossa, the parietal extends forward for a distance of about 120 mm.

Coll. Dub. no. 2795 (? Kedoeng Broeboes) has an angle between the parietal plane and that of the occiput of 110°. The sutures of the parietal on the top of the skull are indistinct, but those in the temporal fossa show it to extend forward to 120 mm from the hinder end of the fossa, the length of the fossa being 140 mm. The most remarkable feature about the present specimen is the great prominence of the crests bordering the hinder ends of the temporal fossae: the least width of the occipital surface between the temporal fossae is 122 mm, but the hinder ends of the temporal fossae are only 100 mm apart. Even so, the temporal contraction is less marked than in any other specimen (table 5).

The surface of the parieto-occipital eminence is damaged; there is, however, a median foramen near the top.

Remaining skull fragments of *Epileptobos* lack the basal portion of the occiput, and have little preserved of the frontals, so that the angles at which the parietal plane is inclined to the frontal or to the occiput cannot be given. They will serve, however, to indicate the individual variation in development of the most salient feature of the *Epileptobos* skull, the parieto-occipital eminence. The horn cores are most often broken off at their bases; occasionally part of one horn core is still attached to a specimen. In all cases, however, the condition of the frontals shows that horn cores have been present.

Coll. Dub. no. 489a, from Kedoeng Broeboes (pl. III fig. 3) is the top of a brain case with the fronto-parietal suture distinctly shown, indenting the frontals at slightly more than a right angle (100°). The median length of the parietal is 65 mm. The sagittal crest is rather steep, and rises into a stout eminence that has a height of 5 cm above the plane of the fronto-parietal sutures, and that falls off abruptly behind, fully in the plane of the occiput. The basal width of the eminence is almost 7 cm; it is situated above the temporal contraction of the occiput (79 mm), and from its base the parietal crests run outward on either side to the postero-internal sides of the horn core bases. The median posterior projection of the eminence is quite marked, as is the crest extending downward from it to the lambdoid crest. On either side of this median crest is a distinct depression, with two small foramina each. One cm above the median posterior projection there are a pair of small foramina, only 2 mm apart, and placed about 25 mm above the level of the basal foramina. Thus, each of the two basal foramina and the upper central foramen on the posterior surface of the parieto-occipital eminence already noticed in Coll. Dub. no. 2786 are duplicated in the present specimen.

Coll. Dub. no. 1696 (Tegoean) represents only a portion of the left frontal with part of the horn core, and the entire parieto-occipital eminence. The horn core measures 95 mm horizontally, and 79 mm vertically in diameters at base. The sutures are indistinct, and the height of the parieto-occipital eminence is approximately 3 cm. The posterior basal depressions are small but distinct. No foramina can be seen in this specimen.

Coll. Dub. no. 2776 (Kedoeng Broeboes), the top of a brain case, very narrow at the temporal contraction (64 mm), has a parieto-occipital eminence 3 cm high, with a short and steep sagittal crest leading up to it. The posterior median projection is very marked, but the posterior basal depressions are hardly visible. There is an upper central foramen.

Coll. Dub. no. 2777 (Kedoeng Broeboes) is similar to the last, except in its less marked temporal contraction (75 mm). The fronto-parietal sutures are clearly shown; the length of the parietal is 63 mm, the sagittal crest emerging immediately behind the median point of the suture.

Coll. Dub. no. 2784 (Kedoeng Broeboes) does not show the fronto-parietal sutures. The sagittal crest of the parietal is very thin transversely, with a sharp edge, and concave on the sides. The parieto-occipital eminence has an upper central foramen, as usual, but in addition there is an even larger foramen, placed more forward, on the anterior slope of the eminence, slightly to the left of the median line. The hinder ends of the temporal fossae are not preserved in this specimen, and the parietal is broken off on either side of the eminence.

Coll. Dub. 2785, the upper part of a brain case from Kedoeng Loemboe, is strongly corroded, without any suture showing. The parietal and temporal crests bordering the temporal fossae are gone, and what is left of the sagittal crest and the parieto-occipital eminence is smoothly rounded off, without any depressions or foramina.

Coll. Dub. no. 2788 (Kedoeng Broeboes) represents the top and left side of a brain case with a powerful parieto-occipital eminence, 4 cm high and about 6 cm wide at base. It has a central upper foramen. The posterior surface is damaged, and does not show the posterior prominence or the basal depressions.

Coll. Dub. no. 2791 (between Dekes and Wadegan) is the upper portion of a brain case, with part of the left horn core attached to it (basal diameters 90 by 78 mm). The parietal crest is damaged at the right side, but the temporal contraction can be determined as 78 mm, and the least width of the occiput at the same level as 88 mm, the difference being due to the prominence of the crest overhanging the end of the fossa. The sagittal crest of the parietal is not conspicuous; it lacks the prominence of that in most of the other specimens. The surface of the parietals slopes evenly upward from the sides and the front to the parieto-occipital eminence without forming an edge in the median line, a true sagittal crest. There is, however, no sudden transition from the surface of the parietals into the eminence (as in Coll. Dub. no. 2793, which has virtually no sagittal crest at all: p. 36); the parieto-occipital eminence has an elevation of 3 cm above the plane of the fronto-parietal sutures, and is only remarkable for its strong posterior prominence, not less than 2½ cm beyond the lambdoid crest. There are two basal foramina behind, below the posterior projection; the distance between these foramina is 18 mm. There is also an upper central foramen.

Coll. Dub. no. 2813 (loc. ?) is another upper portion of a brain case with part of the left horn core, 85 by 78 mm in diameters at base. Above the temporal contraction (85 mm) there rises the parieto-occipital eminence, 5½ cm wide at base, and 2 cm high, with a strong sagittal crest in front of it. The posterior prominence is slightly marked, extending hardly beyond the lambdoid crest. The posterior basal depressions are small, in fact they are only marked by foramina (one on the right, two or three on the left side). The distance between the foramina on both sides of the median line is 23 mm, and they are about 15 mm below the central foramen in the posterior surface of the eminence.

Coll. Dub. no. 2821 (between Dekes and Wadegan), the upper portion of a brain case with part of the right horn core attached to it (diameters ca. 95 by 82 mm) has the frontal and parietal surfaces damaged, while the base of the parieto-occipital eminence, and all of the occiput below it is lost. As far as this state of preservation permits judgment, there seems to have been an inconspicuous sagittal crest on the parietal, as in Coll. Dub. no. 2791; the parieto-occipital eminence has a height of about 3 cm.

Coll. Dub. no. 4584 (Bogo) is the top of a brain case, showing a very strongly developed parieto-occipital eminence that rises 5 cm above the level of the fronto-parietal sutures. Part of the posterior surface of the eminence is broken away, which permits of the observation that the parieto-occipital eminence is hollow inside, occupied by an extensive sinus without a median septum. Whether it communicates with the frontal sinus cannot be ascertained in this specimen (another specimen to be described below shows that it sometimes does); at any rate the sinus extends well into the sagittal crest of the parietal, which is very thick in the present specimen. The sinus is so large that it leaves only a wall of bone less than 1 cm thick on the sides of the eminence. The posterior projection of the eminence is missing, but the basal depressions below it, just above the lambdoid crest, are shown. They are small but deep, and their centres are 30 mm apart. The hinder ends of the temporal fossae are also shown in the present specimen; the temporal contraction is 82 mm.

Coll. Dub. no. 8474 (loc. ?) is a portion of a left frontal with part of the horn core. The sagittal suture of the frontal is partially preserved; the horn core diverges backward at base at an angle of 35° from the median line, and the diverging angle of the horn cores, therefore, was 70°, as usual in *Epileptobos*. The fronto-parietal suture is also preserved, the parietal having broken off just along the suture; it diverges backward from the median line at an angle of 50°, indicating that the parietals indented the frontals at an angle of 100°, as in Coll. Dub. no. 489a. The basal diameters of the core are 88 mm horizontally, and 80 mm vertically.

Coll. Dub. no. 10130 (loc. ?) is the top of a brain case. The horn cores are broken off at base, showing their sinuses. That of the left core has an opening leading from it into the sinus of the parieto-occipital eminence, which is entirely exposed as the upper and posterior surfaces of the eminence have broken away. There is no communication with the sinus of the right horn core, however. The sinus of the parieto-occipital eminence is not divided by a median septum, and it is cut off anteriorly from the frontal sinus (which has a septum in the median line). The wall of the eminence remaining is only 3 mm thick in places, and the sinus clearly involves all of the parietals, extending forward and laterally to where the sutures with the frontals have been. It is cut off from the cranial cavity by bone only a few mm thick, and extends forward into the skull to a distance of 5 cm from the lambdoid crest, that is, about to the level of the fronto-parietal suture which is shown in the roof of the cranial cavity.

The sinus of the parieto-occipital eminence also extends into the external occipital protuberance. the protuberance in the median line just below the lambdoid crest, which is partially broken away, and which proves to be quite hollow, too. The communication is only on the left side, just as is that between the sinus of the parieto-occipital eminence and the frontal sinus at the base of the horn core. This extension of the sinus of the parieto-occipital eminence downward into the external occipital protuberance does not exist in Coll. Dub. no. 4584 dealt with above, however. In the last-mentioned specimen the external occipital protuberance is partially broken off, and is solid.

Parts of the basal depressions just above the lambdoid crest are preserved; the right of these at least has a foramen. These depressions are on a level with the temporal contraction of the skull, which measures 85 mm.

There remain to be described a series of eight skull fragments of *Epileptobos* (Coll. Dub. nos. 11657-11664), each representing the upper portion of a brain case. In all of them the parieto-occipital eminence is preserved, while the horn cores have broken off, parts of their bases raised above the median line of the frontals only remain. The best of these specimens is Coll. Dub. no. 11657, from Bogo, which has most of the left wall of the cranial cavity, and shows a temporal fossa 145 mm long from pterygoid crest to hinder end, the parietal occupying a length of ca. 120 mm. The fronto-parietal sutures indent the frontals at a right angle, and the sagittal crest emerging behind the suture rises into an eminence 3 cm high and 7½ cm wide. Both the posterior projection and the external occipital protuberance have broken off, but the two depressions between them are seen, each with a foramen. The distance between the foramina is 18 mm, and they are about the same distance below the upper central foramen of the eminence. The temporal contraction is 78 mm. In Coll. Dub. no. 11658 (loc. ?), much less complete than the preceding specimen, there is a very prominent sagittal crest on the parietal, with the edge convex anteroposteriorly, leading up to an eminence again 3 cm high by a basal width of 6½ cm. The posterior projection is very marked, but the basal depressions are inconspicuous. The hinder end of the left temporal fossa only remains.

The remaining six specimens (Coll. Dub. nos. 11659-11664) are rather poorly preserved, with more or less heavily corroded surfaces, and all without a record for the exact locality. The fronto-parietal suture is partially seen only in one specimen (Coll. Dub. no. 11659) in which the posterior basal depressions of the parieto-occipital eminence are large; in Coll. Dub. no. 11660 they are quite small. The parieto-occipital eminences in these specimens are not only injured superficially, but parts of them have broken away, sometimes even to a considerable extent (Coll. Dub. no. 11663), which proves beyond any doubt that the parieto-occipital eminences in these specimens are not excavated by sinuses such as those observed in Coll. Dub. nos. 4584 and 10130. As a matter of fact the parieto-occipital eminences in a number of skulls above described are partially damaged, to a sufficient extent to show the presence of a sinus, if any.

It becomes, therefore, evident that the presence of a large sinus in the parieto-occipital eminence of the *Epileptobos* skull is an exception rather than the rule. The majority of the skulls of *Epileptobos* have quite compact parieto-occipital eminences, and for that reason they are usually well preserved. In specimens that are so much injured that the horn cores (which are, of course, extensively excavated in their basal portions by the frontal sinus extending into them) have broken off almost completely, the parieto-occipital eminence remains intact for the most part. It constitutes the most resistant part of the cranium of *Epileptobos*.

To the series of skulls and skull fragments of *Epileptobos groeneveldtii* in the Dubois collection above described I can add one specimen from another collection. In the Cosijn collection from the Djetis (Poetjangan) layers North of Djetis and Perning, Eastern Java, preserved in the Geological Museum at Leiden, there is the top of a brain case of *Epileptobos* (Geol. Mus. Leiden no. 27896). The horn cores are broken off, and the fronto-parietal suture is obliterated, but the parieto-occipital eminence is only slightly damaged. The sagittal crest of the parietal is short but steep, and the eminence has a height of 2½ cm by a basal width of 6 cm. The temporal contraction of the skull is ca. 75 mm; the basal depressions at this level are quite marked. There are two upper central foramina. The posterior projection is not very marked; it extends hardly beyond the lambdoid crest.

The present specimen is similar to many in the Dubois collection already described.

We have now passed in review a total of thirty-eight skulls and skull fragments of *Epileptobos groeneveldtii*, originating from at least twelve localities, viz., Bogo, between Dekes and Wadegan, North of Djetis and Perning, Kebon Doeren, Kedoeng Broeboes, Kedoeng Loemboe, Kedoeng Nojo, Kedoeng Pingit, Tegoean, Trinil, Tritik, and Wadegan. These thirty-eight specimens represent as many individuals, and all of them had horns. There is no skull in the present series, no matter how incomplete, in which the condition of the frontals does not indicate the presence of horn cores. The various species of *Leptobos*, both from Europe and from the Pinjor zone of the Upper Siwaliks, are represented by much smaller series of skulls, and among these there are several hornless skulls, which are those of the females.

There can be no doubt, therefore, that *Epileptobos groeneveldtii* had horns in both sexes, as already surmised by Dubois (1908, p. 1262).

In his original description of the Java *"Leptobos"* Dubois (1908, p. 1261/62) provisionally distinguished a second species of *Leptobos*, which he named *L. dependicornus*, adding, however, that he took it to represent the female of *L. groeneveldtii*. The Trinil skull on which Dubois based his *Leptobos dependicornus* (Coll. Dub. no. 2812), however, belongs to *Bibos*, and represents the female of *Bibos palaesondaicus* Dubois. A description of the specimen will be found on p. 93 of the present work.

The back part of a skull with portions of the horn cores from Djetis figured by Von Koenigswald (1934, p. 193, pl. III figs. 1-2; 1940, p. 62, pl. II fig. 2) as *Leptobos cosijni* resembles the skull Coll. Dub. no. 2766 so very closely that there is no doubt as to their conspecificity.

According to Von Koenigswald (1934, p. 198; 1940, p. 61) *"Leptobos"* would be absent from the Trinil fauna proper, occurring exclusively with the Djetis fauna. As we have seen above, there is one characteristic horn core of *Epileptobos groeneveldtii* in the Dubois collection (no. 2746) that originates from Trinil; this specimen proves that *Epileptobos* formed part of the Trinil fauna proper as the material from Trinil is from the Kaboeh (Trinil) layers and not from the underlying Poetjangan (Djetis) deposits (Duyfjes, 1936, p. 146; Von Koenigswald, 1940, p. 51).

In the course of the above descriptions of the thirty-eight skulls and skull fragments of *Epileptobos* the differences between the various specimens have been noted. There is surprisingly little variation in skull dimensions, or in the diverging angle of the horn cores, which varies only from 65° to 70°. The horn cores themselves are larger and more compressed basally in some specimens than in others, but there are all sorts of intermediate conditions between the two extremes (table 7). The skull with the largest and most compressed horn cores (Coll. Dub. nos. 2833 and 2980) we should expect to be that of a male; those with the horn core almost circular in cross section (Coll. Dub. nos. 2766 and 2829) we should expect to represent females. There is hardly any difference in frontal width between these three skulls, however (210-215 mm); the most slender skull in the present collection (Coll. Dub. no. 2765), a skull that fulfils another requirement which we should expect from the female, has the horn cores more strongly compressed at base than all but two of the others. The amount of curvature of the horn core is almost the same in two skulls (Coll. Dub. nos. 2765 and 2767) that represent the extremes in variation of the width of the frontals.

TABLE 7

Measurements of the horn core of *Epileptobos groeneveldtii*

Coll. Dub. nos.		2833	1696	2765	2775	2791	2767
Length along outer curve		890	—	660+	—	—	—
Horizontal diameter at base		111	95	102	97	90	99
Vertical diameter at base		82	79	86	84	78	87
Index of compression $\left(\frac{\text{vert. x 100}}{\text{hor.}}\right)$		74	83	84	87	87	88
Coll. Dub. nos.	2622	2770	8474	2813	2796	2766	2829
Length along outer curve	750	590+	—	—	—	650	—
Horizontal diameter at base	88	95	88	85	83	94	86
Vertical diameter at base	79	86	80	78	76	89	82
Index of compression $\left(\frac{\text{vert. x 100}}{\text{hor.}}\right)$	90	91	91	92	92	95	95

It is, therefore, clear that the horn cores and the slenderness of the skull do not afford characters of value in discriminating between the sexes in *Epileptobos*. Both sexes carried horns, and there are no clear-cut characters by which the horn cores of the females can be distinguished from those of the males.

The presence of horns in both sexes is one amongst other reasons why I have removed "*Leptobos*" *groeneveldtii* from the genus *Leptobos*, placing it in a distinct genus, *Epileptobos* (Hooijer, 1956b).

Skulls of European Villafranchian species of *Leptobos* have been carefully described by Merla (1949). British Museum skulls of the genotype of *Leptobos*, *Leptobos falconeri* Rütimeyer of the Pinjor zone of the Upper Siwaliks of India, have been described by Rütimeyer (1877-78, pp. 157-165, pl. I figs. 7-8, pl. IV figs. 3-6, pl. VI fig. 9). In 1937 Pilgrim gave a brief description of an American Museum skull of this species (Pilgrim, 1937, pp. 815-818, figs. 45-46). In his monograph on the fossil Bovidae of India Pilgrim (1939, pp. 301-308) presents a formal diagnosis of the genus *Leptobos* as well discussions of *Leptobos falconeri* and of other species of the genus. I have recently studied the British Museum material of *Leptobos falconeri*, and descriptions of this material will be given below. Before passing on to the description of the skull of *Leptobos* proper it is, however, necessary to consider at some length the homologies of the various parts of the parieto-occipital region of the skull in *Leptobos*, *Epileptobos*, and *Bibos*. The following pages are introductory to the comparison of the skull of *Epileptobos* with those of *Leptobos* and *Bibos*.

The structure of the parieto-occipital region of the skull affords several characters by which *Epileptobos* can be distinguished from *Leptobos* of the Villafranchian as well as from *Proleptobos birmanicus* Pilgrim (1913, p. 304), an ancestral form of *Leptobos* from the (?) Dhok Pathan stage on the left bank of the Irrawaddy river near Ava, Burma, fully described and figured by Pilgrim (1939, pp. 309-315, fig. 35). Above all, *Epileptobos* has the median eminence behind the bases of the horn cores that forms the top of the occiput, the parieto-occipital eminence. In *Leptobos* the parietal does not form a high sagittal crest; it is deflected to some extent out of the plane of the frontal, as in *Epileptobos*, but it is not or hardly raised in the median line, and passes into what Pilgrim and Merla call the supraoccipital by another angle, which is either more or less open than the angle between the parietal and the frontal planes. The "supraoccipital", then, is inclined at an open angle to the occipital. Thus, Pilgrim (1939, p. 308) gives three angles for various species of *Proleptobos* and *Leptobos*, the angle between frontal and parietal planes, the angle between parietal and supraoccipital planes, and the angle between supraoccipital and occipital planes. These angles vary from 125°

to 165° (for the angle between frontal and parietal planes Pilgrim rather unaccountably gives the complements instead).

In my descriptions of the various skulls of *Epileptobos* I have given the angle between frontal and parietal planes, and that between parietal and occipital planes, leaving out the "supraoccipital". It should be noted beforehand that Pilgrim evidently encountered some difficulty in measuring the skull of *Epileptobos* in the same way as he had measured those of *Leptobos* proper, for in his table (Pilgrim, 1939, p. 308) the angle between frontal and parietal planes of Coll. Dub. no. 2766 (the holotype of *Epileptobos groeneveldtii*) is not filled in [1]), while the angles at which the "supraoccipital" is inclined to the parietal and to the occipital are given as "? 105°" and "? 170°", respectively. Consequently, in *Epileptobos groeneveldtii* the "supraoccipital" would be inclined to the parietal at little more than a right angle, a less open angle than that in *Proleptobos* and *Leptobos* (125°-155°). The "supraoccipital" would be deflected almost fully into the plane of the occipital instead of being inclined to it at an angle of 125°-140° as in *Proleptobos* and *Leptobos*. It is, therefore, important for us to find out exactly what part of the skull is being referred to by Pilgrim as the supraoccipital.

What, in Pilgrim's opinion, is the supraoccipital, and where does it meet the parietal and the occipital?

Although Pilgrim (1939, p. 147) states that the suture between the parietal and the supraoccipital is indistinct in the specimens of *Leptobos* and *Proleptobos* which he has seen, yet in various places of his work dealing with these genera he refers to the length of the parietal, and to that of the "supraoccipital exposed above the lambdoid crest". In *Leptobos* the parietal is about one-third the length of the frontal (Pilgrim, l.c., pp. 302, 305). The distance between the hinder ends of the temporal fossae is much greater than the length of the supraoccipital exposed above the lambdoid crest (l.c., p. 302); more exactly, less than twice in *L. falconeri* (l.c., p. 305), and as much as three times in *L. elatus* (Pomel) (l.c., p. 307), whereas in *Proleptobos* the two distances are almost equal (l.c., p. 309). It is, of course, only possible to make such statements if the position of the parieto-supraoccipital suture is accurately known.

What Pilgrim considered to be the position of the suture between the parietal and the supraoccipital becomes evident from his description of the skull of *Proleptobos birmanicus*. In this description he indicates the transverse

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1) This angle is 145° in this specimen. It is quite possible that the "150°" given by Pilgrim as the diverging angle of the horn cores of the same specimen actually refers to the angle between frontal and parietal planes and that by some mistake "150°" was placed one line too high in the printed table. The diverging angle of the cores is 65°.

ridge that connects the parietal crests above the temporal fossae as "an approximate boundary between the parietal and the supraoccipital" (l.c., p. 312). The same ridge is referred to a few lines further down as "the parieto-supraoccipital crest".

The transverse ridge in question is also seen on the skull of *Leptobos,* and has already been noticed by Rütimeyer (1867, p. 73) in his description of *L. etruscus* (Falconer). The relevant part of Rütimeyer's description runs as follows: a strong crest emerges immediately behind and below the base of the horn (core); the crests converge rapidly from both sides, joining in the middle of the parietal in a bony eminence. In front of this crest lies the smaller portion of the parietal, which, as in all oxen, indents the frontals posteriorly. Behind this crest lies the proper parietal zone of the upper surface of the skull, bounded laterally by the temporal fossae; the occipital crest lies at the posterior margin of the flat and extensive parietal. The condition thus described is well shown in the figures presented by Rütimeyer (1867, pl. I figs. 3 and 5).

In a subsequent study Rütimeyer (1878, p. 163), describing a skull for *Leptobos falconeri,* writes that the lambdoid suture (the suture between the parietal and the supraoccopital) cannot be distinguished, but that it would have been close to the occipital crest.

Hence it follows that Rütimeyer considered the parieto-supraoccipital suture to coincide with the occipital or lambdoid crest, while Pilgrim regarded the parieto-supraoccipital suture to be at the transverse crest connecting the parietal crests that form the upper boundaries of the temporal fossae. In other words, according to Rütimeyer the supraoccipital does not extend upward beyond the lambdoid crest, while according to Pilgrim the supraoccipital would extend beyond the lambdoid crest, up to the transverse crest connecting the upper boundaries of the temporal fossae.

The transverse ridge in question has been named "ponte intertemporale" by Merla (1949, p. 73), and it will be referred to in the present paper as the intertemporal bridge.

The intertemporal bridge, connecting as it does the upper boundaries of the temporal fossae, is always above and in front of the lambdoid or occipital crest, the latter being the connexion between the temporal crests that form the hinder and lower boundaries of the temporal fossae. The area enclosed by the intertemporal bridge and the lambdoid crest, bounded laterally by the rounded ends of the temporal fossae, forms what Merla (1949, p. 73) calls the "cresta nucale", or nuchal crest.

The distance between the lambdoid crest and the intertemporal bridge varies, of course, with the width of the ends of the temporal fossae. Merla (l.c., p. 144) gives a series of figures from which it can be seen, e.g., that in *Leptobos stenometopon* (Rütimeyer), in which the temporal fossae open more widely on to the posterior surface of the skull than in *L. vallisarni* Merla, the distance between the lambdoid crest and the intertemporal bridge is accordingly greater than that in *L. vallisarni.*

The transverse width of the nuchal crest (Merla, l.c., p. 73) is the distance between the ends of the temporal fossae, the temporal contraction. This distance also varies within *Leptobos*: turning again to the figures of the nuchal crests given by Merla (1949, p. 144) we find that it is much less in *L. stenometopon* than in *L. vallisarni.* The measurements provided by Merla (l.c., p. 112) bear this out; in the type specimen of *L. stenometopon* the distance between the ends of the temporal fossae is 72 mm, and the distance between the lambdoid crest and the intertemporal bridge is 45 mm, while in the type of *L. vallisarni* these two distances are 99 mm and 30 mm, respectively.

We have seen that, in the opinion of Pilgrim, the supraoccipital extends upward to what Merla has called the intertemporal bridge. Hence, the "length of the supraoccipital exposed above the lambdoid crest" (Pilgrim, 1939, pp. 302, 305) is the same as the sagittal diameter of the nuchal crest (Merla, 1949, pp. 73 and 112), from the lambdoid crest to the intertemporal bridge. As follows from the measurements given in the preceding paragraph, in *L. stenometopon* the distance between the ends of the temporal fossae is less than twice that between the lambdoid crest and the intertemporal bridge, whilst in *L. vallisarni* the former distance is as much as three times the latter. This is exactly the same difference as that recorded by Pilgrim (1939, pp. 305, 307) as existing between *L. falconeri* and *L. elatus.*

Merla follows Pilgrim as regards the upward extension of the supraoccipital in *Leptobos;* he states that the surface of the nuchal crest is the plane of the supraoccipital (Merla, 1949, pp. 73 and 113).

Does the supraoccipital in *Leptobos* extend upward beyond the lambdoid crest, as held by Pilgrim and Merla? I do not believe that this is so. There are certain details in the structure of the nuchal crest of *Leptobos* carefully noted by Merla that are also found in *Bibos,* and in that genus they are not on the supraoccipital but on the interparietal instead.

Neither Pilgrim nor Merla mention the role played by the interparietal in the formation of the cranium of *Leptobos,* supposing, as it seems, that the supraoccipital borders on the parietal. This is not so: the interparietal is intercalated between the two.

The interparietals, in *Bibos* as well as in *Bos,* fuse with the parietals and with the supraoccipital before birth or soon after. Their sutures, therefore, are obliterated in the adult but can be observed in skulls of neonati.

I have studied some skulls of neonati of the banteng (*Bibos javanicus*) in the Leiden Museum (reg. nos. 112 and 382; condylobasal length 184 mm). In these specimens the interparietals are united, but the sutures between them and the parietals and the supraoccipital are well shown. The parietals indent the frontals at an obtuse angle (there is a fontanelle at the junction of the coronal (fronto-parietal) and the sagittal sutures in reg. no. 382, which is filled up in reg. no. 112). The parietals, with the interparietal, occupy a transverse band 28 mm wide anteroposteriorly at its narrowest part between the frontals and the supraoccipital, the plane of which is inclined at an angle of about 125° both to the frontal plane and to that of the supraoccipital. The interparietal takes a considerable part in the formation of this zone: it is an almost semicircular bone, fully in the plane of the parietals, with a median length of 17 mm, and a width at base of 40 mm (the width of the brain case is 87 mm). The suture between the interparietal and the supraoccipital runs just along the lambdoid crest, which is a well-marked structure already in the neonatus (for an occipital view of a newborn gaur (*Bibos gaurus* (Smith)) skull see Stehlin, 1893, pl. IV fig. 1).

The interparietal, just above the lambdoid crest, is slightly depressed on either side of the median line, and there is a small foramen in each depression (more distinctly shown in reg. no. 112 than in reg. no. 382). A third foramen may be seen in the median line near the top of the interparietal, half way between the fronto-parietal and the interparieto-supraoccipital sutures. These interparietal foramina, like the parietal foramina in *Homo*, apparently give passage to emissary veins.

A slightly larger skull of *Bibos frontalis* (Lambert) (Leiden Museum, reg. no. 1293; condylobasal length 192 mm) also shows the sutures of the interparietal clearly. The interparietal is a triangular bone, placed just above the lambdoid crest, 46 mm wide at base (the width of the brain case is 96 mm), fully in the plane of the parietals, with a median length of 27 mm, the median length of the parietals in front of it being ca. 25 mm.

In two young skulls of the banteng, with M1 just taken into use (Leiden Museum, cat. ost. d. and f; condylobasal length 36 cm) the sutures between the parietals, interparietal, and supraoccipital are closed. The structure, however, is sufficiently similar to that in the newborn animal to permit of homologization of the various parts with the bones still separated by sutures in the earlier stage. The parietals indent the frontals at an acute angle. The processus corni are well formed (these are mere knobs in the neonatus); from their base a crest curves inward on either side, then downward, and outward again to join the lateral parts of the lambdoid crest. These crests represent the parietal and the temporal crests marking the boundaries of the temporal fossae, which are beginning to take shape.

In the area above the lambdoid crest we observe the interparietal to be deflected somewhat out of the plane of the parietal: the parietal is bent downward on the frontal plane at an angle of 130°, and the interparietal forms a raised triangular area that makes an angle of 150° with the plane of the parietal (an angle of 100° with the frontal plane, that is). Although the parieto-interparietal sutures are closed there can be no doubt that the triangular area just above the lambdoid crest represents the interparietal, for the basal depressions with foramina on either side of the median line are well shown. These foramina are single in cat. ost. d; in cat. ost. f there are several of them at the left, but only one at the right side. Even the third foramen, in the median line, marking the top of the interparietal, does show up, at least in cat. ost. d; it is about half way between the median anterior point of the fronto-parietal suture and the lambdoid crest. In cat. ost. d the raised triangular area representing the interparietal has a width, along the lambdoid crest, of ca. 40 mm (ca. 60 mm in cat. ost. f), the width of the brain case being 105 mm (110 mm in cat. ost. f); the height of the interparietal is 35 mm in both.

In adult skulls of the banteng, recent as well as fossil, many of which will be described in the present paper, the sutures of the interparietal are, of course, obliterated, but the interparietal can often be clearly located. The depressions with foramina just above the lambdoid crest mark the base of the interparietal, and a foramen, occasionally quite distinct, half way between the lambdoid crest and the fronto-parietal suture in the median line marks the top of the interparietal.

These depressions and foramina that characterize the interparietal of *Bibos* have also been noticed in *Leptobos* (Merla, 1949, pp. 73 and 144). The depressions on either side of the median line, between the lambdoid crest and the intertemporal bridge, are called the intermediate fossae (fi in the figures on p. 144 of Merla, 1949). Even the third landmark, the median foramen higher up, is mentioned by Merla (l.c., p. 73), who states that it is placed one cm in front of the intertemporal bridge, and that it is of constant occurrence in the skulls of both sexes.

In my opinion the occurrence of these depressions just above the lambdoid crest, and of a foramen in the median line higher up, is so similar in *Leptobos* to that in *Bibos* as to leave no doubt that they mark the interparietal in the former as well as they do in the latter.

The conclusion following is that in *Leptobos* the supraoccipital extends upward only to the lambdoid crest, the area just above this crest being formed by the interparietal.

We have seen that in *Bibos* the interparietal extends upward in the median line to half way between the lambdoid crest and the frontoparietal suture. There is no skull available of *Leptobos* that shows the parieto-interparietal suture. However, if the median foramen one cm in front of the intertemporal bridge noticed by Merla marks the top of the interparietal, as seems most likely, the interparietal in *Leptobos* does extend to just over the intertemporal bridge. It would, then, occupy the whole of the area of the nuchal crest of Merla's descriptions, between the lambdoid crest and the intertemporal bridge, the area taken by Pilgrim and Merla to represent part of the supraoccipital.

In my descriptions of the skulls and skull fragments of *Epileptobos* I have often mentioned the presence of basal depressions (either with or without foramina) and of an upper central foramen on the posterior surface of the parieto-occipital eminence. After all that has been written above it is clear that the same structural details can be observed in *Bibos* and in *Leptobos*. There can be no doubt that these depressions and foramina in *Epileptobos* are homologous to those in *Bibos* and *Leptobos*, and that they are the landmarks of the interparietal. The intertemporal bridge of *Leptobos* finds its homologue in the median posterior projection of the parieto-occipital eminence of *Epileptobos* that is placed 1-2½ cm below the upper central foramen and just above the basal depressions (the intermediate fossae of Merla's descriptions). On either side of this posterior projection in *Epileptobos* there is a strong ridge connecting it with the parietal crests that run to the bases of the horn cores. The intertemporal bridge thus formed is not straight but is curved upward in its course, and it is a much stronger ridge than the lambdoid crest below it. Between the two there are the intermediate fossae, and above the intertemporal bridge there is the median foramen of the parieto-occipital eminence, corresponding to the median foramen that Merla found to occur one cm in front of the intertemporal bridge in *Leptobos*.

Therefore, in *Epileptobos* the posterior surface of the parieto-occipital eminence, between the lambdoid crest at its base and the central foramen near the top, is formed by the interparietal, which is the "supraoccipital exposed above the lambdoid crest" of Pilgrim's, and the nuchal crest of Merla's descriptions.

Having settled the homologies in the parieto-occipital region of the skull of *Leptobos, Epileptobos,* and *Bibos,* I shall now give the descriptions of the skulls of *Leptobos falconeri* Rütimeyer preserved in the British Museum (Natural History) at London.

The holotype of *Leptobos falconeri* (British Museum (Natural History) no. 40887) is a skull that lacks most of the premaxillaries and that has only the bases of the horn cores, but it is rather well preserved as a whole. The specimen has been figured by Rütimeyer (1877, pl. I figs. 7-8). The sutures, especially those of the lacrimal, are not as clear as would appear from Rütimeyer's figures. The ethmoidal vacuities (not shown in Rütimeyer's figures) are filled with matrix. They occupy the space that in these figures is taken up by the anterior tongue of the frontal, between the nasal and the lacrimal on either side, and they have an anteroposterior extent of 3½ cm by a greatest (posterior) width of 2½ cm.

The nasals are wide (almost 6 cm) and flat in front, and become more convex transversely backward. Between the ethmoidal vacuities they begin to narrow rapidly; they indent the frontals at an angle of about 50°, and their posterior tip extends backward to just beyond the level of the anterior borders of the orbits.

On the maxillaries the infraorbital foramina do not show clearly, but the facial tuberosities are well shown; they are above the junction of P^4 and M^1, and the width of the muzzle over these tuberosities is ca. 150 mm. The lacrimals have a length of about 8½ cm by a height of about 3 cm.

The orbital margins are damaged but do not appear to have been prominent; the width of the skull at the orbits is ca. 220 mm, whereas the postorbital constriction is 212 mm. The orbit is 5 cm in diameter. The supraorbital grooves begin above the orbits, diverging backward and upward along the raised bases of the horn cores. The least distance in between is 8 cm; the position of the supraorbital foramen is not clear in the present skull.

The diverging angle of the horn cores is 65°; the right horn core is preserved up to the border between the pedicle and the horn core proper, while the preserved portion of the left core is even shorter. The bases of the horn cores are raised above the median surface of the frontals, which is slightly arched anteroposteriorly at this level. The right core is more strongly inclined upward than that on the left side; this may be due to some crushing.

Two powerful crests emerge at the posterior inner sides of the horn core bases. These parietal crests converge backward at an angle of about 110° and form the overhanging upper margins of the temporal fossae. Their length from their origin at the base of the horn core to the end of the temporal fossa is almost 9 cm. The hinder ends of the temporal fossae are 50 mm apart.

The fronto-parietal sutures are indistinct in the present specimen; in others to be described below they are seen to be placed just behind the horn core bases, indenting the frontals at an obtuse angle. The surface of the parietal is inclined to that of the frontal at an angle of about 160°. The parietal surface is almost flat; only at the edges it is slightly concave due to the prominence of the parietal crests and of the intertemporal bridge bordering it posteriorly. There is a very weak and narrow sagittal crest on the parietal, a few cm long only; it is shown in the figure presented by Rütimeyer (1877, pl. I fig. 7). The sutures on either side of the sagittal crest indicated in the figure just referred to do not exist, as Rütimeyer (1878, p. 159 footnote) rightly remarks. The coronal (fronto-parietal) suture indicated in the woodcut (Rütimeyer, l.c., p. 159) must be approximately correct in position as it resembles those in other specimens; in the present skull it cannot be observed, however.

The lambdoid crest is quite marked in the skull of *Leptobos falconeri*, and between it and the intertemporal bridge there are the two depressions, the intermediate fossae of Merla (1949, p. 144). The distance between the posterior border of the lambdoid crest and the anterior border of the intertemporal bridge is 40 mm. This distance is 30 mm in the type of *Leptobos vallisarni*, in which the distance between the ends of the temporal fossae is much greater (99 mm) than in that of *Leptobos falconeri* (50 mm). One of the specimens of *Leptobos etruscus* recorded by Merla is very close to the type of *L. falconeri* in width and length of the "nuchal crest", the distance from the posterior border of the lambdoid crest to the anterior border of the intertemporal bridge being 35 mm by a distance between the ends of the temporal fossae of only 45 mm (Merla, 1949, p. 112).

The angles at which the interparietal (the "supraoccipital exposed above the lambdoid crest" of Pilgrim's) is inclined to the parietal and to the occipital are ca. 125° and ca. 140°, respectively. These figures differ slightly from those in *Leptobos etruscus* as given by Merla (1949, p. 66).

The temporal fossae in the holotype of *Leptobos falconeri* are filled with matrix, but they can be studied in other specimens. The dentition is rather well preserved; the right P^2 only is missing, and the outer surfaces of the left P^3-M^1 are incomplete. The M^3 extend backward to just behind the lateral postpalatal notches. In the median line the palate extends backward several cm behind the molars; its edge cannot be clearly seen. The width of the palate between the molars is ca. 75 mm.

Measurements of the present skull of *Leptobos falconeri* are given in table 8; measurements of the premolars and molars are given in table 9.

British Museum (Natural History) no. 39566 is a skull of *Leptobos falconeri* that is eroded all over. The muzzle is incomplete, and the right horn core is broken off. The nasals indent the frontals at an angle of 55°. The ethmoidal vacuities, for the most part cleared off matrix, are as large as those in the preceding skull; the supraorbital grooves are less marked. The fronto-parietal suture, just behind the horn core bases, is distinct; the two parts are slightly curved, with the convexity backward, and meet in the median line at a very obtuse angle. The temporal fossae are cleared off matrix, showing the parietal sutures. The parietal forms a tongue along the upper part of the temporal fossa that extends forward along most of the length of the fossa: the length of the temporal fossa from pterygoid crest to hinder end is 118 mm, and the length of the parietal exposed in the fossa is 100 mm.

The bases of the horn cores are less raised, making the frontals less concave transversely than in the preceding skull. Beside the pedicle, part of the horn core proper is preserved on the left side, but the border is damaged. Because of the erosion of the skull the angles at which the interparietal is inclined to the parietal and to the occiput cannot be given. The dentition is so much damaged that few dental measurements can be given only (table 9). The palate extends 1½ cm behind the posterior borders of M^3 in the median line; the posterior borders of M^3 are 1 cm behind the lateral postpalatal notches. The

TABLE 8

Measurements of the skull of *Leptobos falconeri*

British Museum (Nat. Hist.) nos.	40887	39566	39567	48026	48037	*Epileptobos groeneveldtii*
Median length of frontals	—	ca. 130	142	140	130	175—183
Median length of parietals	—	—	55	60	58	52—77
Width over infraorbital foramina	—	80	91	—	—	93
Width over facial tuberosities	ca. 150	145	153	—	—	150
Distance from orbit to base of horn core	—	—	98	100	—	110—125
Width of frontals at orbits	ca. 220	—	218	225	175	240
Postorbital constriction	212	209	205	213	—	192—216
Diverging angle of horn cores	65°	80°	75°	80°	—	65°—70°
Angle between frontal and parietal planes	ca. 160°	ca. 150°	155°	160°	165°	135°—145°
Idem, parietal and interparietal planes	ca. 125°	—	ca. 115°	125°	135°	—
Idem, interparietal and occipital planes	ca. 140°	—	ca. 160°	145°	135°	—
Angle between parietal and occipital planes	85°	—	95°	90°	90°	110°—120°
Temporal contraction	50	60	60	70	ca. 30	63—100
Greatest width of occiput	202	—	—	197	ca. 140	ca. 220—ca. 250
Width over paramastoid processes	ca. 155	—	ca. 150	162	ca. 120	164—176
Height from basion to lambdoid crest	118	—	ca. 105	100	96	114—128
From upper border of foramen magnum to idem	84	—	ca. 65	65	64	79—95
Width of occipital condyles	100	100	106	105	—	100—112
Width of posterior tuberosities (basioccipital)	66	—	—	66	—	67—75
Width of anterior tuberosities of idem	31	—	—	ca. 30	—	33—42
Width of brain case at middle of temporal fossa	—	114	112	113	—	107—124
Horn core, horizontal diameter at base	71	ca. 64	67	70	—	83—111
Vertical diameter at base	69	ca. 55	64	59	—	76—89
Index of compression $\left(\frac{\text{vert. x 100}}{\text{hor.}}\right)$	97	—	96	80	—	74—95
Length of temporal fossa	—	118	120	—	—	130—155
Length from basion to lateral postpalatal notch	177	182	170	176	150	167—175
Width of palate between M^2	ca. 75	71	80	75	—	84
Height of skull from palatines to nasals	120	128	120	ca. 115	100	130—ca. 135

anterior palatine foramina are on a level with the anterior halves of M^2; the maxillary-palatine suture cannot be seen. The measurements in table 8 indicate that the present skull is very similar to the holotype in size, although the horn cores are smaller and diverge more widely posteriorly.

British Museum (Natural History) no. 39567 (Rütimeyer, 1878, pl. IV figs. 3-4) is a *Leptobos falconeri* skull without the premaxillaries and the nasals. Only the right horn core is preserved for a few cm above the border between pedicle and horn core proper. The lacrimals have a length of 9 cm by a height of 3 cm. The ethmoidal vacuities are well shown, but their nasal border is not preserved. The supraorbital grooves are narrow, running out backward along the raised bases of the horn cores. The position of the supraorbital foramen is clear at least on the right side: it is on a level with the posterior border of the orbit, and 5 cm distant from the median line. The orbital margin is entire on the left side; due to its slight prominence the postorbital constriction is not very marked. The orbit has a diameter of 6 cm.

The fronto-parietal suture is distinct, and indents the frontals at a very open angle as seen in Rütimeyer's figure. The parietal crests are well preserved, converging backward at an angle of about 100°. Their length is 7½ cm, less than that in the holotype. The lambdoid crest is damaged, but the two depressions between it and the intertemporal bridge are distinctly seen. The skull base is imperfect. Some dental measurements can be given (table 9).

British Museum (Natural History) no. 48026, like the foregoing specimen, has only part of the right horn core above the pedicle preserved. The skull is broken off anteriorly at the level of the anterior borders of M^1. The parietal crests are almost 8 cm long, and converge backward at an angle of 100°, as in the preceding skull, although the distance between the hinder ends of the temporal fossae is greater (70 mm) than in that specimen (60 mm). The distance from the posterior border of the lambdoid crest to the anterior border of the intertemporal bridge is about 30 mm. Almost the same figures obtain in two *Leptobos etruscus* skulls (Merla, 1949, p. 112: length over lambdoid crest and intertemporal bridge 28-29 mm; width between ends of temporal fossae 66-68 mm).

The present skull is broader at the frontals than any other British Museum skull of *Leptobos falconeri,* only the American Museum skull is larger still (Pilgrim, 1937, p. 818). The right horn core is grooved longitudinally; the grooves indicate a faint counter-clockwise torsion.

There is a fifth male skull of *Leptobos falconeri* in the British Museum (Natural History) (no. 17141), not noticed by Rütimeyer. It is less complete than the others, most of the postorbital region on the right side being broken away. So far as can be seen it does not differ from the skulls above described, and hence it does not need special comment. A detached basal portion of the horn core bearing the same catalogue number has a maximum diameter of 78 mm.

The female skull of *Leptobos falconeri* (British Museum (Natural History) no. 48037) described and figured by Rütimeyer (1878, pp. 162-165, pl. IV figs. 5-6, pl. VI fig. 9) is almost completely preserved. The dentition is in an excellent state of preservation (table 9). The skull is slightly crushed; it has been subjected to pressure from the side which makes the width measurements somewhat unreliable. The absence of horn cores is its most important character. Because of this there is no postorbital constriction, the skull being widest at the orbits.

The present female skull is as a whole smaller than the male; the length of the parietal is proportionally greater, while the interparietal is somewhat less deflected into the occipital plane, and the temporal contraction is more marked than in the males (table 8). These differences, however slight, indicate a more primitive condition in the female than in the male skull, as has already been pointed out by Merla (1949, p. 82) in his notes on the female skull of *Leptobos etruscus*.

None of the British Museum skulls of *Leptobos falconeri* has the horn core preserved very far above the base; in the American Museum skull of that species described by Pilgrim (1937, pp. 815-818) only the upper portions of the horn cores are lacking, and these have been restored "with a reasonable

TABLE 9

Measurements of upper teeth of *Leptobos falconeri*

British Museum (Nat. Hist.) nos.	40887	39566	39567	48026	48037
P^3, anteroposterior	18	—	—	—	17
transverse (top)	19	—	—	—	15
idem (alveolus)	21	—	—	—	19
P^4, anteroposterior	—	—	—	—	—
transverse (top)	17	—	—	—	16
idem (alveolus)	22	—	—	—	22
M^1, anteroposterior	—	—	—	—	21
transverse (top)	—	—	—	20	19
idem (alveolus)	26	—	—	26	—
M^2, anteroposterior	30	—	29	27	27
transverse (top)	24	—	21	20	19
idem (alveolus)	30	—	27	26	25
M^3, anteroposterior	30	—	—	28	29
transverse (top)	24	—	—	19	19
idem (alveolus)	29	27	—	—	26
Length P^2-P^4	57	57	—	—	53
Length M^1-M^3	82	88	92	—	76

approach to accuracy" (Pilgrim, l.c., p. 817). They are seen to curve backward and outward at first, with the convexity inward, but in their upper half they are bent upward somewhat out of the frontal plane. As restored, the horn core of the American Museum specimen of *Leptobos falconeri* is longer than that in any other species of *Leptobos*. Among the male skulls of the various species of *Leptobos* there are very few that have the horn core entire; the measurements given in table 10 are taken from Pilgrim (1937, p. 818) as far as *Leptobos falconeri* is concerned, while those of European species are taken from Merla (1949, pp. 72, 104, and 107)).

TABLE 10

Measurements of the horn core in *Leptobos* species

	L. falconeri	*L. etruscus*	*L. vallisarni*	*L. stenometopon*
Length along outer curve	ca. 590	500	330	420
Horizontal diameter at base	85	79	88	72
Vertical diameter at base	77	73	77	58
Index of compression $\left(\frac{\text{vert. x 100}}{\text{hor.}}\right)$	91	92	88	81

As will be seen from table 7, in which the measurements of the horn cores of *Epileptobos groeneveldtii* are given, the cores are longer in the Java form than in *Leptobos,* the entire cores varying in length along the outer curve from 650 mm to 890 mm. Added to that they are thicker at the base than those in *Leptobos* with the exception only of those in the largest *Leptobos falconeri* skull and in the type of *L.vallisarni,* which fall within the variation range of *Epileptobos* in this respect. The horn cores both of *Leptobos etruscus* and of *Leptobos vallisarni* remain in the frontal plane, and differ in curvature from those of *Epileptobos,* their convexity being outward (Merla, 1949, p. 71 fig. 2) instead of inward. The horn cores of *Leptobos stenometopon* are for the most part above the frontal plane, and have the convexity inward, curving forward and inward at the tip (see Rütimeyer, 1867 pl. I figs. 3-4; Merla, 1949, pl. VIII fig. 1) as in *Epileptobos*. However, the entire horn core of *L. stenometopon* is only two-thirds as long as the shortest entire core in *Epileptobos*.

The index of compression of the horn core at base (table 8) varies from 80 to 97 in *Leptobos falconeri,* a variation range that includes Merla's observations on the European species of *Leptobos* given above (81-92). *Epileptobos* varies between even wider limits, viz., 74-95. The index of compression, therefore, does not appear to be of value as a diagnostic character.

The diverging angle of the horn cores in *Leptobos falconeri* varies from

65° to 80°. In the European specimens of *Leptobos* recorded by Merla (1949, pp. 72, 104, and 107) this angle varies from 83° (in a specimen of *L. stenometopon*) to 100° (in *L. etruscus* and in *L. vallisarni*). Pilgrim (1939, p. 308) gives the diverging angle of the cores as 120° in a specimen of *L. etruscus,* and even 130° for a specimen of *L. elatus.* It follows from this that the cores diverge at a wider angle in the European species of *Leptobos* than in *L. falconeri* of India. In *Epileptobos groeneveldtii* of Java the angle of divergence of the horn cores is remarkably constant, varying only from 65° to 70°, which is within the variation limits of *L. falconeri.* In Pilgrim's table of measurements the diverging angle of the horn cores in the skull of *Epileptobos groeneveldtii* Coll. Dub. no. 2766 is given as 150° (Pilgrim, 1939, p. 308), which is a mistake; it is only 65°. Possibly "150°" was placed one line too high in Pilgrim's table, and actually refers to the angle between the frontal and the parietal planes in this specimen, which would be approximately correct. However this be, there is no base for Pilgrim's statement (l.c., p. 307) that in the Leiden skulls the divergence of the cores is much greater than in *L. falconeri.*

The slight counter-clockwise torsion (for the right horn core) is a character in which *Epileptobos* agrees with *Leptobos* proper (Pilgrim, 1939, p. 301; Merla, 1949, p. 113).

The horn cores in *Epileptobos* are shifted farther behind the orbits than in *Leptobos*; this is a progressive character (cf. Pilgrim, 1939, p. 142). The distance between the orbit and the base of the horn core is 125 mm in the holotype of *Epileptobos groeneveldtii*; that in the skull British Museum (Nat. Hist.) no. 48026 as well as that in the American Museum skull of *Leptobos falconeri* (Pilgrim, 1937, p. 818) is only 100 mm, whilst the width of the skull at the constriction between orbit and horn core is practically the same in the three cases (213-215 mm). A narrower skull of *Leptobos falconeri* (British Museum (Nat. Hist.) no. 39567), with a postorbital constriction of 205 mm, has a distance between orbit and horn core base of 98 mm, again less than one-half the least frontal width. In the shifting backward of the horn core to the degree that the distance between orbit and base of horn core exceeds one-half the least frontal width *Epileptobos* marks a step from *Leptobos* toward *Bibos javanicus,* the banteng, in which the distance from orbit to horn core base is always more than one-half the least frontal width (table II).

The structure of the parieto-occipital region of the skull is clearly more advanced in *Epileptobos* than in *Leptobos.* The parietal in *Leptobos falconeri* is less reduced in size than in *Epileptobos*; in the former it indents the frontal at a very obtuse angle, while in the latter, just as in *Bibos,* the parietal indents the frontal at approximately a right angle or less. In *Leptobos falconeri* the median length of the parietal is still about two-fifth the median length of the frontal in the males (British Museum (Nat. Hist.) nos. 39567 and 48026), and even almost one-half the frontal length in the female (British Museum (Nat. Hist.) no. 48037; see table 8), whereas in *Epileptobos* (Coll. Dub. nos. 2765 and 2829, see table 5) the median length of the parietal is less than one-third that of the frontal.

In *Leptobos* the parietal is still on the upper surface of the skull, taking a considerable part in the upper surface of the brain case; the angle between the frontal and the parietal planes varies from 140° (in *L. vallisarni*: Merla, 1949, p. 103) to 165° (in the female of *L. falconeri*). In *Epileptobos* the parietal is less extended than that in *Leptobos*, and the angle between frontal and parietal planes varies only from 135° to 145° (table 5). In *Bibos* the parietal is deflected fully in the plane of the occiput, and the angle between the frontal and the parietal planes is approximately a right angle in the females, but it is less than 80° in the males, the females thereby displaying the more primitive condition.

In *Leptobos* the parietal is not or hardly raised in the median line, just as in *Bibos*, whereas in *Epileptobos* the parietal forms a marked sagittal crest. In *Leptobos* the parietal is inclined to the interparietal at an angle that varies from 120° (in *L. vallisarni*: Merla, 1949, p. 67) to 155° (in *L. elatus*: Pilgrim, 1939, p. 308). In *Epileptobos* the plane of the parietal (which is the plane of the fronto-parietal sutures on either side of the sagittal crest) is inclined to that of the interparietal at approximately the same angle as that at which it is inclined to the occipital plane; this angle is 110°-120° (table 5). In *Bibos* the parietal is in the same plane as the interparietal, of which it forms an upward extension.

In *Leptobos* the interparietal is inclined to the occipital plane at an angle that varies from 125° (in *L. elatus*: Pilgrim, 1939, p. 308) to 160° (in *L. vallisarni*: Merla, 1949, p. 67). In *Epileptobos* this angle is approximately 180° as the posterior surface of the parieto-occipital eminence that is formed by the interparietal is an extension of the occiput above the lambdoid crest, in the same plane as the occiput. It is just the same in *Bibos*, the interparietal being fully in the plane of the occiput.

Thus, while the parietal is still on the upper surface of the skull in *Epileptobos*, as in *Leptobos*, the interparietal in *Epileptobos* is deflected fully into the plane of the occiput, as in *Bibos*. In this respect *Epileptobos*, again, marks a step from *Leptobos* toward *Bibos*.

In his diagnosis of the genus *Leptobos* Pilgrim (1939, p. 302) states that the temporal fossae open on to the "supraoccipital" only, while in *Bibos*, "the temporal fossae open widely on to that portion of the occiput which extends far above the occipital crest, and includes both the supraoccipital and the parietal" (l.c., p. 320). The last statement is correct if we substitute interparietal for supraoccipital, but the first statement remains incorrect even if we read interparietal for supraoccipital. As is evident from Merla's description of the skull of *Leptobos etruscus* the parietal enters into the formation of the temporal fossa, extending forward along most of the length of that fossa (Merla, 1949, p. 75). I have already noted the same condition in my description of the skull of *Leptobos falconeri* (British Museum (Nat. Hist.) no. 39566). Therefore, the crest that forms the upper boundary of the temporal fossa is on the portion of the occiput formed by the parietal, and the temporal fossae do open on to the interparietal and the parietal in *Leptobos* just as they do in *Epileptobos* and in *Bibos*.

In *Leptobos falconeri* the hinder ends of the temporal fossae approach one another on the occiput somewhat more closely than in *Epileptobos*. The ratio of the temporal contraction to the width of the brain case at the middle of the temporal fossa varies in *Leptobos falconeri* from 0.53 (British Museum (Nat. Hist.) no. 39566) to 0.62 (British Museum (Nat. Hist.) no. 48026), whereas in *Epileptobos* this ratio varies from 0.66 (Coll. Dub. no. 2786) to 0.84 (Coll. Dub. no. 2795). In *Bibos* the hinder ends of the temporal fossae approximate to one another to a less degree; there are several recent skulls of *Bibos javanicus* in which the least width of the occiput between the temporal fossae even exceeds the width of the brain case (table II).

The occiput as a whole is wider in *Epileptobos* than in *Leptobos falconeri* (table 5). There is, however, no difference in brain case width. The height of the skull from palatines to nasals in *Epileptobos* is in excess of that in *Leptobos falconeri*. The height of the occiput in *Epileptobos* also exceeds that in *Leptobos falconeri* with the exception only of the skull British Museum (Nat. Hist.) no. 40887; the height measurements of the occiput of this skull are within the variation limits of those of *Epileptobos* (table 8). While the occiput in *Leptobos* is more or less semicircular, that of *Epileptobos* has a triangular shape, the top being formed by the parieto-occipital eminence that is such a salient feature of the skull of the Java form.

Coming now to the dentition, comparison between tables 6 and 9, presenting dental measurements of *Epileptobos* and *Leptobos falconeri* respectively, will reveal that in the latter the transverse diameters at the alveolar margin are decidedly in excess of those taken at the top of the worn crowns, while in *Epileptobos* this difference is much less. It follows therefore that the premolars and molars of *Epileptobos* are more hypsodont than those of *Leptobos* *falconeri.* In fact, as shown in table 6, the teeth of *Epileptobos* are as hypsodont as those in the female banteng (*Bibos javanicus*), which are of the same size as those in the fossil Javan form. For this reason it has been found impossible to definitely assign any lower dentitions to *Epileptobos*; there are no mandibular rami associated with any of the *Epileptobos* skulls, and the few well-preserved rami of the mandible of large bovines in the Dubois collection belong either to *Bubalus* or to *Bibos*. Of the remaining, fragmentary specimens no identification is possible; with a view to the abundance of skulls of *Epileptobos* it is likely that many actually represent the mandible of this form, but in the absence of distinguishing features they must be left unidentified.

The only postcranial remains that can be assigned to *Epileptobos* are an atlas and a left metacarpal associated with the skull from Kedoeng Nojo (Coll. Dub. no. 2765). The wings of the atlas are damaged, but the greatest width does not seem to have exceeded 200 mm; the least ventral length is 47 mm, which makes for a length-width ratio of at least 0.24. This is a figure that falls in the lower end of the range of variation for this ratio in fossil *Bibos* atlases (table 15). The metacarpal, the distal end of which is missing, measures 64 mm in proximal width, which is within the limits of recent *Bubalus* and *Bibos* specimens (table 16). A fossil *Bubalus* metacarpal has a proximal width of 83 mm; the metacarpal of *Bibos palaesondaicus* is unknown but was probably narrower than that of *Bubalus palaeokerabau.* Because of the incomplete state of the specimens from Kedoeng Nojo nothing of value for purposes of discrimination can be deduced from them beyond the conclusion that the postcranial skeleton of *Epileptobos* probably resembled that of *Bibos* more closely than that of *Bubalus,* a conclusion that could not possibly be contradicted by, but in fact already follows from the study of the skull.

Genus HEMIBOS Rütimeyer

The full history of the genus *Hemibos* and the intricate synonymies of its three Siwalik species have already been given by Pilgrim (1939, pp. 259-269). I have seen the holotypes of *H. triquetricornis, H. acuticornis,* and *H. antelopinus* in the British Museum (Nat. Hist.). It is to the first and second of these that two Dubois collection skulls belong. These specimens were collected in 1895 in the Siwaliks of the Punjab, and will now be considered.

Hemibos triquetricornis Rütimeyer

Coll. Dub. no. 3107, collected at Mahrawala, 2½ miles N.E. of Haripoor on the Somb Nuddy, Sirmur State, Punjab (pl. IV fig. 1) is a skull with the horn cores broken off at their bases, and deformed as a result of pressure; the right maxillary region is crushed, and the snout in front of the infraorbital foramina is missing. However, the two mandibular rami are preserved with the skull; at the right side the condyle of the mandible is still in the glenoid cavity, and at the left side it is only 3 cm out of its cavity. The left ramus is thrust forward and inward, the right downward and outward, and both have broken off anteriorly in front of P_2. It is because of this rare association of the skull and the mandible that the present specimen deserves some attention, for it does belong to the best known species of Siwalik bovines, *Hemibos triquetricornis,* of which there are not less than twenty-four skulls in the British Museum collection (Rütimeyer, 1878, p. 122). Naturally, there is a great deal of variation in this series, a variation that is apparently individual. As Pilgrim (1939, p. 263) points out, the skulls have all been found at approximately the same horizon (assumed to be the Pinjor zone of the Upper Siwaliks) and in the same locality.

The Dubois collection specimen of *Hemibos triquetricornis,* its defects notwithstanding, appears to belong to the Aepyceros form (Rütimeyer, 1878, p. 128); the frontals are narrowed and rather concave transversely between the horn cores, and the orbits project far beyond the general outline of the skull. When viewed from above the parietal is more shortened than that in the normal form (Rütimeyer, l.c., pl. VII fig. 1).

In table 11 I have followed Pilgrim (1939, p. 269) in the choice of measurements; on comparing this table with Pilgrim's our specimen will be seen to be rather broad at the orbits and at the mastoid. The length of the lower molars and premolars (not recorded by Pilgrim) does not exceed that in the domestic Java water buffalo, although the mandibular ramus is rather stouter in the premolar region.

Pilgrim (l.c., p. 264) states that the lower premolar series is less reduced in *Hemibos* than in *Bubalus,* but in the present specimen of *Hemibos* (Coll. Dub. no. 3107) I find the anterior lower premolar, P_2, much reduced in size and, in fact, almost indistinguishable from its homologue in recent *Bibos javanicus* (see below, p. 73).

Hemibos acuticornis (Falconer et Cautley)

The second *Hemibos* skull collected by Dubois around Haripoor in the Punjab (Coll. Dub. no. 3043; pl. IV fig. 4) comprises only the fronto-occipital portion and the base of the left horn core. The orbits are very imperfect; in front of them the skull is broken off. The left horn core base shows that the cores diverged at less than a right angle, and are less tilted backward than

TABLE 11

Measurements of the skull of *Hemibos*

	H. triquetricornis	*H. acuticornis*
Coll. Dub. no.	3107	3043
Distance from fronto-nasal suture to fronto-parietal suture	ca. 160	—
Distance from fronto-parietal suture to summit of occipital crest	—	85
Length of temporal fossa	—	ca. 125
Breadth of brain case	—	ca. 115
Breadth of skull at orbits	230	ca. 180
Breadth of skull at mastoid	ca. 220	ca. 180
Width of occipital condyles	ca. 100	ca. 100
Height of occipital from bottom of occipital condyles to summit of occipital crest	ca. 125	ca. 100
Height of face at M^3	ca. 140	—
Distance between supraorbital pits	ca. 100	—
Diverging angle of horn cores	—	ca. 75°
Angle between parietal and frontal planes	—	140°
Length of upper molar series	95	—
M^3, antero-posterior diameter	35	—
Length of lower molar series	ca. 105	—
Length of lower premolar series	60	—

in *H. triquetricornis*; the cross section is subtriangular with rounded antero-internal and postero-external keels and a sharp inner keel. The frontals are concave between the cores, and the fronto-parietal suture is approximately a right angle, situated about 9 cm in front of the occipital crest. The parietal meets the frontal at an angle of 140°. The specimen, the measurements of which are given in table 11, agrees rather well with two British Museum skulls measured by Pilgrim (1939, p. 269). Like *H. triquetricornis*, the present species is admittedly from the Pinjor zone of the Upper Siwaliks; four specimens, including the type, have been figured by Rütimeyer (1877, pl. III).

Genus BUBALUS Smith

Bubalus palaeokerabau Dubois

Bubalus buffelus, (*B. palaeindicus*) Dubois, Natuurk. Tijdschr. Ned. Indië, vol. 51, 1891, p. 94.

Bubalus palaeokerabau Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1263.

Buffelus palaeokerabau, Stremme, in L. Selenka and M. Blanckenhorn, Die Pithecanthropus-Schichten auf Java, Leipzig, 1911, p. 124, pl. XVIII figs. 5-6, pl. XIX fig. 8, pl. XX figs. 7-9, 14.

Bos (*Bubalus*) *bubalis palaeokerabau*, Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Indië, no. 23, 1933, p. 95; De Ing. in Ned. Indië, vol. 1, sect. IV, 1934, p. 194; Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 52, 1935, p. 542; Wet. Med. Dienst Mijnb. Ned. Indië, no. 28, 1940, p. 61.

Buffelus bubalus? var. *sondaicus fossilis* Van der Maarel, Wet. Med. Dienst. Mijnb. Ned. Indië, no. 15, 1932, p. 25, pl. I figs. 1-4.

Bos (*Bubalus*) cf. *bubalis* Von Koenigswald, De Ing. in Ned. Indië, vol. 1, sect. IV, 1934, p. 194.

? *Bos* spec., Stehn and Umbgrove, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 46, 1929, pl. IV figs. 6-7.

The recent water buffalo of Java is a domestic animal. As already surmised by Schlegel and Müller (1845, p. 207) no truly wild buffalo occurs in the Malay Archipelago; those found in a semi-wild state are derived from domesticated specimens. The question immediately arises how much the tame animals have changed in captivity, or what their immediate wild ancestors were like. The wild Indian buffalo or arni, from which the domestic buffalo is generally thought to have been derived, is a much larger animal, with enormous horns; in fifteen specimens recorded by Lydekker (1898, p. 122) the length along the outer curve varies from 138½ cm to 196½ cm. The largest horn in our collection from Java (Leiden Museum, cat. ost. l) measures 98 cm along the outer curve. The horn core length in this specimen is only 41 cm.

There is a buffalo on the island of Soemba remarkable for the great length and outward direction of the horns, which turn backward only toward the tips, the tip to tip interval being almost 3 m ('t Hoen, 1921, p. 2/3, fig. 3; Merkens, 1927, p. 96; Dammerman, 1928, p. 312; Van der Maarel, 1932, p. 35/36; Dammerman, 1934, p. 489). However, this peculiar horn development, as Wegner (1950) has pointed out, results from an operation performed when the animals are about two years old. The young buffaloes are castrated, and an incision is made on the dorsal surface of each horn, 2 to 3 cm in length (at this stage of growth the length of the horn is about 10 cm: Merkens, 1927, p. 107). As a result of this artifice the horns grow into the shape and size noted above. "The ownership of one or more of these showy animals increases the importance of the owner considerably in the eyes of the people. I have been told that one of these buffaloes has been exchanged for no less than 100 common specimens, but generally speaking they are not for sale" (Wegner, l.c., p. 709). It is evident that such monstrosities should be excluded if we are using recent skulls for comparison with fossil forms to which they may be related.

There is an arni skull from Hindostan in the Leiden Museum (*Bubalus bubalis,* cat ost. d) 1) the right horn of which can be removed; it measures

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1) A note on the label of this specimen reads: "Ind. fig. dans Shaw. Gen. Zoöl.". In his General Zoology, Shaw (1801) presents two figures of the arni, both of which, however, are copied from Kerr's Animal Kingdom (1792). Kerr's work contains the

113 cm along the outer curve, and the length of the core is 83 cm. A right horn also from Hindostan (Leiden Museum, cat. ost. f) has a length along the outer curve of 103 cm by a core length of 84 cm. The skull is quite adult, and though its horns are much shorter than those of the arni recorded by Lydekker (op. cit.) they are within the limits of six specimens figured by Inverarity (1895, pls. A-C), which vary in horn lengths round the curve from 104 to 145 cm (l.c., p. 41). The arni horns exceed in size those of recent *Bubalus* from Java, including the so-called "wild" buffaloes dealt with by Dammerman (1934, p. 491) that do not differ significantly from the "tame" specimens, and should be regarded as merely feral.

The arni skull in the Leiden Museum also surpasses the recent *Bubalus* skulls from Java in basilar length (basion-prosthion: 575 mm); in this respect the recent arni skull is quite close to some of the fossil skulls from Java named *Bubalus palaeokerabau* by Dubois, which will be described in the following pages.

Coll. Dub. no. 60, originating from Trinil (pl. IV fig. 2) is a skull that has one of the premaxillaries in place, and possesses both horn cores, entire up to their tips. Its defects notwithstanding it is the best preserved skull of *Bubalus palaeokerabau* in the Dubois collection, the holotype of the species. The dorsal surface of the skull is well preserved, the left orbit is entire, and most of the left zygomatic arch is preserved. The occiput is incomplete on the right side, the skull base is imperfect, of the dentition only M^{2-3} dext. are in situ, and the left premaxillary has broken off.

The facial portion of the skull is slender relative to the cranial portion; its profile is nearly straight. The nasals, which have bifid anterior ends with the lateral point longer than the median, are in contact with the premaxillaries for a length of about 5 cm. The nasals are very weakly convexo-concave from before backward, and but slightly arched transversely. The supraorbital

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earliest available name for the wild buffalo of India, *Bos arnee* Kerr (1792, p. 336), Linnaeus's *Bos bubalis* having been based on the domesticated form (Harper, 1940, p. 326). The first of these figures of the arni (Kerr, 1792, plate facing p. 295, lower figure; Shaw, 1801, pl. 210 facing p. 400; Vasey, 1857, p. 105) represents the entire animal, and is stated by Kerr (l.c., p. 336) to be a copy of "a Mogul painting in the possession of the late Mr. Ross of Edinburgh". The horns are rather slender, and curved in an almost circular fashion, quite unlike those in the Leiden skull. The second figure (Kerr, 1792, plate facing p. 336, upper lefthand figure: Shaw, 1801, pl. 210 facing p. 400, righthand figure) represents a skull with the horns the whereabouts of which are not given but which probably is in the Edinburgh College Museum. In the latter specimen the span of the horns is about 134 cm, the interval between the tips about 33 cm, as opposed to 105 cm and 61 cm, respectively, in the Leiden Museum arni skull. In another skull partially shown in Kerr's plate (not copied by Shaw) the horns do not curve inward at their tips, the interval between which is about 114 cm. Hence, it is quite clear that the Leiden Museum skull is not among those figured by Kerr and by Shaw.

TABLE 12 Measurements of the skull of *Bubalus bubalis* (domestic) from Java and of the arni

					♂	♀		Arni
Leiden Museum	cat.a	cat. b	cat. j	cat. l	no. 1046	no. 1046	no. 4897	cat. d
Basilar length (basion-prosthion)	505	510	475	500	450	445	450	575
Facial length (prosthion-nasion)	320	320	275	325	280	280	270	355
Cranial length (nasion-basion)	255	250	245	255	235	230	235	305
Facial length index $\left(\frac{\text{facial length x 100}}{\text{basilar length}}\right)$	63	63	58	65	62	63	60	62
Cranial length index $\left(\frac{\text{cranial length x 100}}{\text{basilar length}}\right)$	50	49	52	51	52	52	52	53
Width of frontals at postorbital constriction	205	210	180	195	180	175	180	230
Skull width-length index $\left(\frac{\text{postorbital constriction x 100}}{\text{basilar length}}\right)$	41	41	38	39	40	39	40	40
Width of muzzle at level of naso-premaxillary notch	110	115	90	95	95	85	90	115
Muzzle width index $\left(\frac{\text{muzzle width x 100}}{\text{basilar length}}\right)$	22	22	19	19	21	19	20	20
Length from basion to lateral post-palatal notches	190	185	180	180	170	165	170	225
Length from posterior border of orbit to posterior base of horn core	140	150	115	140	115	110	110	205
Width of occipital condyles	105	105	100	105	95	100	75	135
Width of occiput over paramastoid processes	180	180	160	180	165	150	140	215
Least width of occiput between temporal fossae	90	90	65	85	75	70	65	135
Width of brain case at middle of temporal fossae	125	125	115	125	115	110	110	135
Height of occiput from basion to lambdoid crest	100	100	100	100	95	95	95	140
Height of skull from palatines to nasal	140	145	130	135	130	120	125	160
Horn core, horizontal diameter at base	—	—	65	90	80	60	60	165
Idem, vertical diameter at base	—	—	40	60	60	40	40	95
Basal circumference of horn core	—	—	170	245	230	165	160	460
Core length along the outer curve	—	—	250	420	290	210	200	830
Straight length from anterior base to tip	—	—	220	410	245	190	185	740
Interval between tips of horn cores	—	—	ca. 550	ca. 1020	525	460	460	—
Index of length $\left(\frac{\text{outer curve x 100}}{\text{width of frontals}}\right)$	—	—	139	215	161	120	111	361
Index of proportion $\left(\frac{\text{outer curve x 100}}{\text{circumference}}\right)$	—	—	147	171	126	127	125	180
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	—	—	114	102	118	111	108	112
Index of compression $\left(\frac{\text{vert. diam. x 100}}{\text{horizontal diam.}}\right)$	—	—	62	67	75	67	67	57

grooves are shallow and divergent behind; the supraorbital foramina are just behind the orbits, and 15 cm apart. The orbits, the greatest (anteroposterior) diameter of which is 7 cm, are only a very short distance in front of the horn cores (4 cm approximately). The frontal profile is convex anteroposteriorly as well as transversely between the horn cores; just behind the horn cores it falls off into the occipital surface without, however, forming a marked skull vertex. The surface is rugose.

The horn cores are subtriangular in cross section; their upper surface is flat, and the anterior angle is sharply defined. The posterior angle is less well marked, and the inferior angle is very smoothly rounded. The cores diverge backward at an angle of almost 180°, and curve outward and backward in a very regular curve. They do not remain in the frontal plane but slope gently downward: when the skull is lain on a table, resting on the occipital condyles and the molars, the tips of the horn cores just touch the table-top. Full measurements of the present skull will be found in the first column of table 13.

A comparison with the recent domestic water buffalo of Java and with the arni (measurements in table 12) reveals that the fossil skull from Trinil is much wider behind the orbits relative to the basilar length; the skull width-length index is 48 in the fossil as opposed to only 38-41 in the recent water buffalo. Further, the horn cores are much larger relative to the frontal width in the fossil than in the recent domestic water buffalo of Java (horn core length index 365 against 111-215); in this respect the Pleistocene *Bubalus* from Java agrees with the recent arni, in which the index in question is 361. By its size, the fossil skull from Trinil agrees with that of the recent arni, the dimensions of which are far in excess of those of the recent domestic water buffalo of Java.

The above are the most essential distinguishing characters of *Bubalus palaeokerabau*. In his diagnosis of the species, Dubois (1908, p. 1263) deals mainly with the horn cores, and states the skulls of the fossil and living water buffalo species of Java to be very similar, a statement that is not borne out by the craniometrical data presented above.

Coll. Dub. no. 61 (Trinil) is a skull complete down to the ends of the premaxillaries but with neither of the horn cores entire, and the palate detached from the skull (but separately preserved under Coll. Dub. nos. 3806 and 9416). The present skull is almost as long as, but narrower behind the orbits than the preceding specimen (table 13). The rugosities on the frontal between the horn core bases are less pronounced. The horn cores are not as heavy as those of Coll. Dub. no. 60, and less compressed at base. All these differences, however, most probably are of a sexual nature only.

Distal portions of the right (Coll. Dub. no. 3011) and of the left horn core (no. 3247) fit on to the core portions attached to the skull but the tips are incomplete; the length of a core along the convex curve is 83 cm as preserved, and would have been several cm longer in the complete state. Their upper surface is flat, even slightly concave in the middle part; the anterior and lower surfaces remain convex throughout. The anterior upper edge is sharp, the posterior edge is rounded basally but becomes sharply defined in the distal half of the core. The lower edge is rounded proximally and distally, but is rather well-marked in the middle of its course. The cores are regularly curved outward and backward, and are less drooping than those in Coll. Dub. no. 60; even when complete the tips would not have extended to the plane passing through the ventral surfaces of the occipital condyles and the molars.

The occiput is entire but for the paroccipital processes; the condyles project but slightly backward, and the portion of the occiput below the lambdoid crest is decidedly lower than that in Coll. Dub. no. 60. Because of the rounded skull vertex the total height of the posterior surface of the skull has not been taken; the distance from basion to nasion shows that the cranial length of Coll. Dub. no. 61 is decidedly less than that in the holotype specimen.

On the ventral surface of the skull, the posterior tuberosities of the basioccipital are seen to be much extended transversely, while the anterior tuberosities are elongate in shape. The union of the vomer and the palatines cannot be observed in the present skull.

Coll. Dub. no. 3468 is the only remaining *Bubalus* skull from Java in the Dubois collection of which the basilar length can be taken; it has the left premaxillary in place. This skull is longer than either of the two already described, but in skull width-length index it is intermediate (table 13). Of the horn cores belonging to the present skull the left (Coll. Dub. no. 2748) is entire, the right (no. 3010) incomplete. The horn core is proportionally longer than that in Coll. Dub. no. 60, and more curved, too.

Coll. Dub. no. 57, originating from Soember Kepoeh, consists of two horn cores and the portion of the frontal between their bases only. The specimen is remarkable for the great length of the cores, the tip to tip interval being not less than 1650 mm. In proportion both to the frontal width and to the basal circumference the length round the curve exceeds those of all the other skulls in the collection.

Coll. Dub. no. 59 (Trinil), a fronto-occipital skull portion, has the right horn core almost entirely preserved, while the distal third of the left core is missing. The orbits are incomplete, although the posterior end of the nasals is shown, and the palate has broken off. The right horn core has a length round the curve of 87 cm, and probably was 10 cm longer in the complete

TABLE

Measurements of the skull of

Coll. Dub. nos.	60 (type)	61	3468	57	59
Basilar length (basion-prosthion)	540	530	560	—	—
Facial length (prosthion-nasion)	340	350	335	—	—
Cranial length (nasion-basion)	300	270	300	—	295
Facial length index $\left(\frac{\text{facial length x 100}}{\text{basilar length}}\right)$	63	66	60	—	—
Cranial length index $\left(\frac{\text{cranial length x 100}}{\text{basilar length}}\right)$	56	51	54	—	—
Width of frontals at postorbital constriction	260	230	260	270	—
Skull width-length index $\left(\frac{\text{postorbital constriction x 100}}{\text{basilar length}}\right)$	48	43	46	—	—
Width of muzzle at level of naso-premaxillary notch	110	100	110	—	—
Muzzle width index $\left(\frac{\text{muzzle width x 100}}{\text{basilar length}}\right)$	20	19	20	—	—
Length from basion to lateral post-palatal notches	205	—	—	—	—
Length from posterior border of orbit to posterior base of horn core	195	175	200	—	185
Width of occipital condyles	—	135	130	—	130
Width of occiput over paramastoid processes	—	210	220	—	225
Least width of occiput between temporal fossae	120	90	ca. 130	—	115
Width of brain case at middle of temporal fossae	145	140	—	—	140
Height of occiput from basion to lambdoid crest	135	120	ca. 130	—	125
Height of skull from palatines to nasal	165	—	170	—	—
Horn core, horizontal diameter at base	160	130	160	—	145
Idem, vertical diameter at base	105	95	105	100	105
Basal circumference of horn core	440	365	450	470	420
Core length along the outer curve	950	—	1020	1170	—
Straight length from anterior base to tip	880	—	860	1010	—
Interval between tips of horn cores	1425	—	—	1650	—
Index of length $\left(\frac{\text{outer curve x 100}}{\text{width of frontals}}\right)$	365	—	392	433	—
Index of proportion $\left(\frac{\text{outer curve x 100}}{\text{circumference}}\right)$	216	—	227	249	—
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	108	—	119	116	—
Index of compression $\left(\frac{\text{vert. diam. x 100}}{\text{horizontal diam.}}\right)$	66	73	66	57	72

state. Its upper surface is slightly raised instead of flat, and the lower edge is very sharply marked off anteriorly by a deep groove that originates about 10 cm from the base and continues to almost 70 cm from the base. In the left core the lower edge is much less pronounced, and the longitudinal groove does not show. In both cores, however, the anterior upper edge is sharp, and the posterior rounded, as usual.

13

Bubalus palaeokerabau

64	73	71	2938	62	63	66	72	2991	2847	58	67	2843
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	305	—	300	300	300	—	—	—	270	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
250	—	230	—	250	245	245	—	—	ca. 220	230	210	210
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	100	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	205	215	—	—	—	—	—	—	—	—	—
200	—	180	—	200	195	190	—	—	—	160	—	—
—	130	130	130	125	120	—	125	125	120	—	—	—
230	—	230	225	—	—	—	200	—	—	—	—	—
145	110	120	115	105	130	—	—	100	—	—	90	95
145	150	135	—	145	140	150	—	135	—	—	—	130
ca. 125	120	130	125	115	120	—	120	130	—	—	—	—
—	—	160	—	—	—	—	—	—	—	—	—	—
165	170	140	—	160	160	150	140	150	110	125	135	105
110	120	100	—	105	105	90	90	105	70	85	90	75
465	480	405	—	450	445	390	385	415	305	350	360	305
1020	1000	—	—	—	—	—	—	—	—	610	590	670
910	890	—	—	—	—	—	—	—	—	570	530	600
—	—	—	—	—	—	—	—	—	—	970	830	850
408	—	—	—	—	—	—	—	—	—	265	281	319
219	208	—	—	—	—	—	—	—	—	174	164	220
112	112	—	—	—	—	—	—	—	—	107	111	112
67	71	71	—	66	66	60	64	70	64	68	67	71

In the present specimen the horn cores are not drooping: they remain in the plane of the frontals throughout.

Coll. Dub. no. 64 (Trinil), likewise a fronto-occipital skull fragment, holds the entire left horn core, and only the basal part of the right. The cores are slightly inclined downward beyond the frontal plane while curving outward and backward, and the apical portion of the left core is seen to curve upward to a slight extent. Due to the prominence of the temporal crests the least width of the occiput between the temporal fossae is equal to the width of the brain case at the middle of the temporal fossae; usually the least occiput width is much less than the brain case width.

Coll. Dub. no. 73 (Trinil) is a fronto-occipital skull part with the left horn core (Coll. Dub. no. 2668) detached but complete, and the base of the right core (no. 4781) broken. The horn cores are heavier at the base than those of any other *Bubalus* skull in the Dubois collection.

Two skulls, Coll. Dub. nos. 71 and 2938, both from Trinil, lack the muzzle and most of the horn cores, but have the palate in place. The palatal portion of Coll. Dub. no. 71 is registered as no. 2955. The median posterior extension of the palate beyond the lateral postpalatal notches, and the fusion between the vomer and the palatines are shown.

Coll. Dub. nos. 62 and 63, both Trinil specimens, possess the basal parts of both horn cores but lack the palate. The posterior end of the nasals is present, and so are the occipital condyles. In cranial length and in basal core diameters the skulls agree with the holotype, but the hinder ends of the temporal fossae approach each other much more closely in no. 62 than in no. 63, the type being intermediate in this respect.

Coll. Dub. no. 66, another Trinil specimen, has the bases of both horn cores, but the occiput has broken off at the temporal constriction. Coll. Dub. no. 72 (Trinil), and Coll. Dub. no. 2991 (between Dekes and Wadegan) have the basal portion of one horn core only, the left in no. 72, the right in no. 2991 (registered as no. 3018), and almost the whole of the occiput.

There remain four *Bubalus* skulls in the collection that are worth mentioning because of their rather small dimensions as compared with those already referred to above. The measurements will be found in the last four columns of table 13. Coll. Dub. no. 2847 (Kedoeng Broeboes), to which belong the left horn core no. 3002, and the facial part no. 616, is an adult skull as shown by the presence of M^3. The horn cores are incomplete apically, so that their length cannot be determined, but their basal diameters are less than those in any of the above mentioned specimens. Coll. Dub. nos. 58 (Trinil), 67 (Tritik), and 2843 (Trinil) fortunately possess both horn cores complete up to their tips, showing that the cores not only are smaller at base, but also shorter than those in the above described specimens (index of length 265-319 as opposed to 365-433). In their regular outward and backward curve, shape of the cross section, and amount of compression at base the cores do not differ from the larger specimens. The entire horn cores of Coll. Dub. nos. 58, 67, and 2843 average shorter in proportion to their basal girth than those of the larger specimens first described (index of proportion 164-220 against 208-249), but longer than those of the recent domestic water buffalo of Java (index of proportion 125-171). The horn cores of the smaller fossil specimens, however, agree with those of the larger fossil specimens in being decidedly longer relative to the frontal width than those of the recent domestic *Bubalus bubalis,* and I believe that the smaller fossil skulls are not entitled to more than a varietal distinction from *Bubalus palaeokerabau.*

Of the present species there are a great number of fragmentary skulls in the Dubois collection, mostly fronto-occipital portions without the horn cores and with the occiput partially preserved only. These specimens are the following: Coll. Dub. nos. 65 (Ngloewak, Solo valley), 68 (Trinil), 69 (Trinil), 70 (loc. ?), 295 (loc. ?), 543 (Tegoean), 2773 (loc. ?), 2779 (Kedoeng Broeboes), 2782 (Kedoeng Broeboes), 2806 (Kedoeng Broeboes), 2814 (loc. ?), 2815 (Kedoeng Broeboes), 2818 (Kedoeng Broeboes), 2827 (loc. ?), 2837 (Kali Gedeh), 2838 (loc. ?), 2840 (loc. ?), 2841 (loc. ?), 2842 (Trinil), 2844 (Trinil), 2845 (Trinil), 2846 (Tegoean), 2870 (Trinil), 2871 (Kedoeng Broeboes), 2872 (Kedoeng Broeboes), 2873 (loc. ?), 2874 (loc. ?), 2875 (loc. ?), 2876 (loc. ?), 2877 (loc. ?), 2878 (Trinil), 2880 (Tegoean), 2882 (loc. ?), 2883 (Tegoean), 2885 (Trinil), 2886 (Trinil), 2888 (Bogo), 2936 (Trinil), 2939 (Tritik), 2940 (Kali Gedeh), 2941 (Kali Gedeh), 2942 (Kali Gedeh), 2944 (Kali Gedeh), 2946 (Kali Gedeh), 2947 (Kali Gedeh), 2948 (Kali Gedeh), 2950 (loc. ?), 2952 (Trinil), 2953 (Kedoeng Broeboes), 2956 (Trinil), 2957 (Kedoeng Broeboes), 3006 (Trinil), 3007 (Trinil), 4348 (loc. ?), 3469 (loc. ?), 3470 (loc. ?), 3805 (Trinil), 4436 (Pati Ajam), 4501-4505 (Trinil), 4507 (Trinil), 4511 (Trinil), 4617-4618 (Tegoean), 4892 (Kali Gedeh), 4901 (Tegoean), 8091 (loc. ?), 10546-10547 (Trinil), 10554 (loc. ?), 10963 (Bangle), 11125 (loc. ?), and 11205 (Kedoeng Broeboes).

Fragmentary horn cores of *Bubalus* are registered as follows: Coll. Dub. nos. 363 (loc. ?), 444 (loc. ?), 575 (loc. ?), 2867 (loc. ?), 2949 (Kali Gedeh), 2954 (Trinil), 2963 and 6574 (one specimen, Kedoeng Broeboes), 2969 (Bogo), 2970 (Kali Gedeh), 2971 (loc. ?), 2989 (loc. ?), 2992 (loc. ?), 2993 (Kedoeng Broeboes), 2996 (Tegoean), 3000 (Kedoeng Broeboes), 3009 (loc. ?), 3014 (Pati Ajam), 3015 (between Dekes and Wadegan), 3019 (Trinil), 3020 (Trinil), 3021 (Trinil), 3241 (Trinil), 3487 (loc. ?), 3492-3493 (loc. ?), 4261 (loc. ?), 4346 (Tawang), 4437 (Pati Ajam), 4650 (loc. ?), 4851 (Trinil), 6573 (Kedoeng Broeboes), 8475 (? Tegoean), 10151 (loc. ?), 10155 (loc. ?), 10272 (loc. ?), 10349 (Bangle), 10385 (Kedoeng Broeboes), and 11283 (loc. ?).

A survey of all the cranial material of *Bubalus palaeokerabau* recorded above, described and undescribed, shows that the larger specimens such as the type are decidedly more common. The Trinil skull described by Stremme (1911, p. 124, pl. XX figs. 7-9) has horn cores almost 90 cm long. A specimen from Bondol recorded by Van der Maarel (1932, p. 25, pl. I figs. 3-4) has a horn core length of ca. 1140 mm; another specimen, from Pitoe, recorded by the same author, has a core length round the curve of ca. 1260 mm, exceeding the largest Dubois collection specimen, which measures 1170 mm round the curve. In the Ngandong fauna of Java (Upper Pleistocene) there are even larger specimens: a skull from Ngrawoh has a tip to tip interval of 225 cm (Von Koenigswald, 1940, p. 63). The presence of adult *Bubalus* skulls with small and graceful horn cores (Trinil, Kedoeng Broeboes) is also noted by Von Koenigswald (l.c.), but of these no measurements have been given.

As already noticed by Dubois (1908, p. 1263) *Bubalus palaeokerabau* differs from *Bubalus palaeindicus* (Falconer) from the Narbada Beds (see Falconer, 1868 I, pl. XXII figs. 1-3) in the horn cores having a less outward direction and being more curved; in cross section, moreover, the horn cores of the Java fossil *Bubalus* are not subquadrangular as they are in the Narbada form. *Bubalus platyceros* Lydekker (1877, p. 31) from the Upper Siwaliks (Pinjor zone and Boulder Conglomerate), fully described by Lydekker (1878, pp. 127-132, pl. XVIII) and by Rütimeyer (1877-78, pp. 138-140, pl. II figs. 4-5, as *Bubalus sivalensis*) differs from the fossil Java *Bubalus* in the horn cores being directed obliquely upward and triangular in cross section. It should be noted, however, that Pilgrim (1937, p. 822, figs. 48-50) has described and figured an Upper Siwalik skull as *Bubalus* cf. *platyceros* that makes a very decided approach to *Bubalus palaeindicus,* and that forms almost a connecting link between the two fossil Indian species.

The mandible of *Bubalus* differs from that of *Bibos* in being longer and more slender, higher at the teeth, with a wider but relatively lower ascending portion; the coronoid process in *Bubalus* is wider and apparently more strongly recurved backward and outward than that in *Bibos* (Stremme, 1911, p. 128, pl. XIX figs. 8-9). Two Trinil specimens (Coll. Dub. nos. 540 and 336, pl. V figs. 1-2) illustrate these differences; the first is a *Bubalus,* the second a *Bibos* mandibular ramus, from the right side. The coronoid process is missing in Coll. Dub. no. 540 but is shown in Stremme's specimen (Stremme, l.c., pl. XIX fig. 8) that lacks the angular process fully preserved in our specimen. As may have been expected from the difference in size between the skulls of *Bubalus palaeokerabau* and those of the recent domestic water buffalo of Java, the Trinil mandible of *Bubalus* is larger than any of the

TABLE 14

Measurements of the mandible of *Bubalus palaeokerabau* and of *Bubalus bubalis* (domestic) from Java

	Bubalus palaeokerabau Coll. Dub. no. 540	*Bubalus bubalis* recent, Java
Length of ramus from mental foramen to hinder surface of angle	390	310-340
Length P_3-M_3	150	125-145
Height of ascending ramus from lower surface of angle to mandibular notch	190	125-155
Height of ramus behind M_3	105	70-85

recent *Bubalus* mandibles from Java, although it differs from the mandible of *Bibos* in the same points as the recent *Bubalus* mandibles do (table 14).

The mandibular rami of *Bubalus* and *Bibos* from Trinil mentioned above are the most complete specimens in the Dubois collection; in both of them as well as in the two Trinil specimens figured by Stremme (1911, pl. XIX figs. 8-9) the anterior premolar, P_2, has broken off. It so happens that P_2 is the only tooth that serves to distinguish between the dentitions of *Bubalus* on the one hand, and *Bibos* on the other. There are no reliable differences in structure between the upper or lower premolars and molars of the two genera *Bubalus* and *Bibos* (see Colbert and Hooijer, 1953, pp. 118-120) except for the fact that the P_2 of *Bibos* has suffered more reduction than that of *Bubalus* (l.c., p. 118, pl. 32 figs. 2-5). This difference was found when comparing the dentitions of Pleistocene *Bibos gaurus* and *Bubalus bubalis* from China, and it proves to hold well in the case of *Bibos palaesondaicus* and *Bubalus palaeokerabau* from the Pleistocene of Java also. In *Bibos* P_2 is smaller and lower-crowned than in *Bubalus*; its outer wall is convex anteroposteriorly, whereas in *Bubalus* there is an outer vertical groove in the posterior third of the crown of P_2 just as in P_3 and P_4. The anterior wing of P_2 is more prominent, and the posterior inner valley is much deeper in *Bubalus* than in *Bibos*. Two slightly worn recent left P_2s, of *Bibos javanicus* (Leiden Museum, reg. no. 15398) and of *Bubalus bubalis* (Leiden Museum, cat. ost. c), respectively, do show these differences very clearly (pl. V figs. 5-10).

In most of the fossil mandibular rami in the Dubois collection the diagnostic anterior premolar unfortunately has broken away. In these specimens the preserved portion of the bone of the mandible usually is too small to determine with certainty whether it belongs to *Bubalus* or to *Bibos*. However, in those cases in which the P_2 is still in situ it is either of the *Bubalus* or of the *Bibos* type. The following fossil ramus fragments can be referred to

Bubalus palaeokerabau: Coll. Dub. nos. 357 (Trinil), 2596 (Trinil), 2958 (Trinil), 4459 (Trinil), 8140 (Trinil), 8480 (Kedoeng Broeboes), 9000-9002 (Kali Gedeh), and 9024-9025 (Bangle). One of these (Coll. Dub. no. 2598) is figured on pl. V fig. 3 above a lower dentition of *Bibos palaesondaicus* to show the difference in size and structure of the anterior premolars in the two genera. Of the fossil P_2s of *Bubalus palaeokerabau* the largest (Coll. Dub. no. 2598) measures 18 mm in length and 11 mm in width; the smallest (Coll. Dub. no. 8140) measures 15 by 10 mm. The range of variation in size of P_2 in recent *Bubalus bubalis* from Java is: length 13-16 mm, width 9-10.5 mm.

For the study of the fossil postcranial remains there are available two recent skeletons of *Bubalus bubalis* (Leiden Museum, cat. ost. a and c), and five skeletons of *Bibos javanicus*. Of the recent banteng skeletons, three are of male individuals (Leiden Museum, cat. ost. a, cat. ost. h, and reg. no. 13133) and two of females (Leiden Museum, cat. ost. b and c). I have found reliable differences in proportions between *Bubalus* and *Bibos* in the atlas and in the metapodials only; there are no consistent differences between the other vertebrae or foot bones of *Bubalus* and *Bibos*. Of the limb bones, a slight difference in relative proximal and distal widths is apparent only in the tibia; the other long bones do not differ in proportions and hence cannot be definitely assigned either to *Bubalus* or to *Bibos* as isolated fossils.

The difference between the atlases of *Bubalus* and *Bibos* is quite conspicuous, and has already been noticed by Stremme (1911, p. 133 ,fig. 7 A and B). In *Bubalus* the wings extend more outward and backward than in *Bibos*. This difference can be expressed in figures: in the ratio of the least ventral length to the greatest width recent *Bubalus* varies from 0.21 to 0.22, and recent *Bibos* from 0.27 to 0.33 (table 15). Twenty-eight well-preserved fossil atlases in the Dubois collection likewise fall into two categories; their measurements are given in table 15 also. All of the fossil specimens originate from Trinil with the exception of Coll. Dub. nos. 8918 and 10584, which are from Kedoeng Broeboes, of nos. 9259-9260, which are from Tritik, and no. 11648, which is from Koewoeng near Ngandong, Solo Valley (the latter specimen was presented by Mr. P. D. Burggraaf in 1948). The fossil atlases of *Bubalus* are decidedly larger than the recent, and vary between wider limits. There is almost no overlap in dimensions or ratios between the atlases of *Bubalus palaeokerabau* and of *Bibos palaesondaicus*, which differ from each other in the same points as those of the recent water buffalo and of the banteng do.

The metacarpals of *Bubalus* are shorter and more expanded distally than those of *Bibos*, as is evident from table 16.

TABLE 15

Measurements of the atlas of recent and fossil *Bubalus* and *Bibos*

	Least ventral length	Greatest width	Length-width ratio
Bubalus bubalis			
Leiden Museum, cat. a	44	208	0.21
cat. c	36	162	0.22
Bubalus palaeokerabau			
Coll. Dub. no. 11648	44	295	0.15
7555	52	292	0.18
7846	54	290	0.19
7059	55	286	0.19
9124	45	284	0.16
7694	51	282	0.18
8092	55	280	0.20
7730	50	280	0.18
7729	56	274	0.20
7895	48	267	0.18
7554	53	245	0.22
7790	50	242	0.21
7341	48	237	0.20
7519	52	232	0.22
Bibos javanicus			
Leiden Museum, cat. a	51	176	0.29
cat. h	53	186	0.28
reg. 13133	57	211	0.27
cat. b	49	152	0.32
cat. c	48	147	0.33
Bibos palaesondaicus			
Coll. Dub. no. 7595	56	242	0.23
7340	54	236	0.23
3036	55	234	0.24
7831	56	223	0.25
7060	47	216	0.22
9260	58	214	0.27
7768	57	209	0.27
9259	53	205	0.26
7896	53	200	0.27
9131	57	195	0.29
10584	51	192	0.27
7620	45	189	0.24
8864	55	180	0.31
8918	51	171	0.30

The two fossil metacarpals of *Bubalus palaeokerabau*, both from the right side and originating from Pengilon near Kedoeng Broeboes, are not only larger but also relatively wider distally than their homologues in *Bubalus bubalis*; in this respect they even surpass the *Bubalus* metacarpals from the Middle Pleistocene of Yenchingkou, Szechwan, China, in which the ratio of distal width to length varies from 0.42 to 0.46 (Colbert and Hooijer, 1953, p.

TABLE 16

Measurements of the metacarpal of recent and fossil *Bubalus* and *Bibos*

	Length	Proximal width	Middle width	Distal width	Ratio: Distal width / length
Bubalus bubalis					
Leiden Museum					
cat. a	173	68	40	74	0.43
cat. c.	175	61	35	66	0.38
Bubalus palaeokerabau					
Coll. Dub. no.					
10514	208	—	59	103	0.50
10515	195	83	56	ca. 95	ca. 0.49
Bibos javanicus					
Leiden Museum					
cat. a	233	72	42	67	0.29
cat. h	241	72	44	66	0.27
reg. 13133	237	73	45	69	0,29
cat. b	215	59	36	56	0.26
cat. c	219	60	34	56	0.26

121). There are no entire *Bibos* metacarpals in the Dubois collection; four fossil *Bibos* metacarpals from Yenchingkou vary in distal width-length ratio from 0.25 to 0.32 (l.c., p. 126).

The tibia of *Bubalus* differs from that of *Bibos* in its slightly greater relative proximal and distal widths. This difference, however slight, enables us

TABLE 17

Measurements of the tibia of recent and fossil *Bubalus* and *Bibos*

	Length	Proximal width	Distal width	Proximal width/length ratio	Distal width/length ratio
Bubalus bubalis					
Leiden Museum					
cat. a	332	108	72	0.33	0.22
cat. c	314	101	65	0.32	0.21
Bubalus palaeokerabau					
Coll. Dub. no. 8743	415	134	88	0.32	0.21
2621	400	140	90	0.35	0.23
Bibos javanicus					
Leiden Museum					
cat. a	407	122	73	0.30	0.18
cat. h	410	117	74	0.29	0.18
reg. 13133	426	122	78	0.29	0.18
cat. b	352	109	67	0.31	0.19
cat. c	361	108	66	0.30	0.18
Bibos palaesondaicus					
Coll. Dub. no.					
10502	412	125	80	0.30	0.19

to distinguish between the fossil tibiae. There are three entire tibiae in the Dubois collection, all from the left side. Coll. Dub. no. 8743 (Trinil) agrees with the recent *Bubalus* tibiae in proportions; Coll. Dub. no. 2621 (Tandjoeng near Solo) is more expanded at both ends, and thereby differs even more from *Bibos* tibiae. The single fossil *Bibos* tibia (Coll. Dub. no. 10502, Trinil) is within recent limits (table 17).

The metatarsals of *Bubalus* and *Bibos* differ in the same way as the metacarpals do (table 18). Two left metatarsals from Trinil (Coll. Dub. nos. 1624 and 1654) can be safely referred to *Bubalus palaeokerabau,* although their distal expansion is less than that in the *Bubalus* metatarsals from Yenchingkou, Szechwan, China (ratio of distal width to length 0.37-0.38: Colbert and Hooijer, 1953, p. 121) it is decidedly greater than that in *Bibos.* There are, again, no fossil *Bibos* metatarsals in the Dubois collection; those from Yenchingkou vary in distal width-length ratio from 0.20 to 0.25, much as the recent do (l.c., p. 126).

TABLE 18

Measurements of the metatarsal of recent and fossil *Bubalus* and *Bibos*

	Length	Proximal width	Middle width	Distal width	Ratio: Distal width/length
Bubalus bubalis					
Leiden Museum					
cat. a	200	62	39	70	0.35
cat. c	204	52	31	61	0.30
Bubalus palaeokerabau					
Coll. Dub. no. 1624	245	63	44	76	0.31
1654	246	60	42	71	0.29
Bibos javanicus					
Leiden Museum					
cat. a	267	61	36	63	0.24
cat. h	260	60	39	62	0.24
reg. 13133	271	59	38	65	0.24
cat. b	238	54	31	56	0.24
cat. c	241	52	32	53	0.22

Bubalus bubalis (L.) subsp.

In the Dubois collection from limestone caves in Central Sumatra there are isolated teeth of large bovines and of caprines. The cave fauna is of no great age; all the species present are recent, and are living today either in Sumatra or in Java or in both. The age of the Central Sumatran cave fauna is post-Pleistocene. No remains of domestic animals have been found in the cave collection, however, and there is no evidence of human inhabitation in the caves either.

The large bovine teeth are in part those of the banteng, *Bibos javanicus* (d'Alton), which is now extinct in Sumatra (see p. 98) but the water buffalo has also been present in prehistoric Sumatra. In the collection of teeth from the Sibrambang cave, Central Sumatra, there is a P_2 dext. that has all the characters of the recent anterior lower premolar of *Bubalus*: there is a posterior outer groove, the crown is more hypsodont, the anterior wing more prominent, and the posterior inner valley deeper than in *Bibos*. The specimen (Coll. Dub. no. 809 c) is figured on pl. IX fig. 2 below a recent P_2 of *Bubalus bubalis* from Java (Leiden Museum, reg. no. 4897). The subfossil specimen measures 18 mm anteroposteriorly, and 11 mm transversely, dimensions which exceed those of the P_2 in the domestic Java water buffalo (length 13-16 mm, width 9-10.5 mm), and which agree with those of the largest P_2 of *Bubalus palaeokerabau* in the Dubois collection from the Pleistocene of Java (Coll. Dub. no. 2598). Larger still is the P_2 of *Bubalus bubalis* from the Middle Pleistocene of Yenchingkou, Szechwan, China (19 by 12 mm: Colbert and Hooijer, 1953, p. 120).

The recent water buffalo of Sumatra is either domestic or feral. Does the cave P_2 represent an aboriginally wild water buffalo, or does it belong to an animal that has already been domesticated? The same uncertainty obtains with regard to the recent water buffaloes found in parts of the Malay Peninsula and Borneo; it is too much to suppose that a single *Bubalus* tooth found in a cave could provide a definite answer one way or the other. We know that the cave teeth tend to be larger than their recent homologues; we know also that no domestic animal remains have been found in the Sumatran caves but only those of truly wild species. It is more likely than not that the prehistoric Sumatran water buffalo represents an indigenous form; it may be provisionally recorded as *Bubalus bubalis* (L.) subsp.

Genus BIBOS Hodgson

Bibos palaeosondaicus Dubois

Bison sivalensis Martin, Samml. Geol. Reichsmus. Leiden, vol. 4, 1887, p. 61, pl. VII fig. 2.

Bibos banteng Dubois, Natuurk. Tijdschr. Ned. Indië, vol. 51, 1891, p. 94.

Bibos, Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 24, 1907, p. 454.

Bibos palaesondaicus Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1262; Hooijer, Zool. Med. Museum Leiden, vol. 34, no. 17, 1956, p. 240, Mammalia, vol. 22, 1958, p. 74.

Bibos palaeosondaicus, Stremme, in L. Selenka and M. Blanckenhorn, Die Pithecanthropus-Schichten auf Java, Leipzig, 1911, p. 136, pl. XVIII fig. 7, pl. XIX figs. 9-10, pl. XX figs. 10-11, 15.

Bibos cf. *palaeosondaicus* (pro parte), Umbgrove, in Cosijn, Verh. Geol. Mijnb. Gen. Ned. en Kol., Geol. Ser., vol. 9, 1931, p. 119.

Bos (Bibos) banteng palaeosondaicus, Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Indië, no. 23, 1933, p. 93.
Bibos protocavifrons Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1262; Soergel, Palaeontographica, suppl. 4, part 3, 1913, p. 2; Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Indië, no. 23, 1933, p. 94.
L[eptobos] dependicornus Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1261/62.
Leptobos dependicornis, Pilgrim, Mem. Geol. Surv. Ind., new series, vol. 26, 1939, p. 303.
Leptobos dependicornus, Hooijer, Zool. Med. Museum Leiden, vol. 34, no. 17, 1956, p. 240.
Bibos sondaicus fossilis Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Indië, no. 15, 1932, p. 42, pl. II figs. 1-5, pl. III figs. 1-4.

As follows from the above synonymy Dubois originally recorded the fossil *Bibos* from Java as *Bibos banteng.* In his final account of the fossil bovid material from Java Dubois (1908, p. 1262), however, writes that several forms of *Bibos* are represented; those more or less closely resembling the living banteng he takes together as *Bibos palaesondaicus.* Besides, a fossil form deceivingly similar to the gaur is named *Bibos protocavifrons.* The living gaur, *Bibos gaurus* (Smith), does not occur in Java but is distributed from the Malay States and Indo-China to Burma and India; a Pleistocene race has been described from Southern China (Colbert and Hooijer, 1953, p. 122). The gaur differs from the banteng mainly in the excessive development of the intercornual ridge at the skull vertex and the anteroposterior concavity of the frontal surface, although these characters are not very marked in the vanishing Malay race (Chasen, 1940, p. 204). The presence of a gaur-like bovine in the Pleistocene of Java, therefore, would be of interest from a zoogeographical point of view, but in point of fact *Bibos protocavifrons* has only once been recorded since (in a paper without any description or figure: Soergel, 1913), and has been provisionally considered identical with the living banteng by Von Koenigswald (1933, p. 94). *Bibos palaesondaicus* is considered a valid species by Stremme (1911, p. 139), but it is regarded as a subspecies of the living banteng by Von Koenigswald (1933, p. 93), who found that in the fossil form the females are less markedly differentiated from the males than in the recent.

For comparison with the fossil material of *Bibos* in the Dubois collection I have used the extensive series of skulls and skeletons in the Leiden Museum, comprising the material described by Schlegel and Müller (1845) as well as a large series of wild Java banteng skulls recently acquired from Mr. M. Bartels. In reading Rütimeyer's chapters on the banteng and the gaur (Rütimeyer, 1867, pp. 77-105) it should be kept in mind that the skull described as that of a young male (l.c., pp. 80, 86, and 101/102, second column in tables) in fact is that of an adult female. The same mistake was made before by

Schlegel and Müller (1845, p. 208, *Bos sondaicus,* pl. 38 fig. 5), and afterwards by Jentink (1887, p. 128, *Bibos banteng,* c). The skeleton in question, as shown by the teeth and horns as well as by the fused epiphyses of the bones and the roomy pelvis belongs to an adult female individual (Hooijer, 1956a, p. 224).

The valid name of the recent banteng is *Bibos javanicus* (d'Alton), 1823, antedating *Bos sondaicus* and *Bos banteng* by 19 and 21 years, respectively. The full history of the nomenclature of the recent banteng is given in Hooijer (1956a) and need not be retold here. The holotype is an adult male skeleton sent in 1821 by Reinwardt from Java to the Leiden Museum (cat. ost. a).

The extensive material of the recent banteng available for direct comparison with the fossil specimens consists of 26 adult male and 5 adult female skulls, all originating from Java. The females differ widely from the males in their smaller size, relatively less elevated intercornual ridge, and in the development of the horns, which not only are considerably smaller than those of the male individuals but also diverge less widely behind, and in themselves are straighter, proportionally shorter and more conical than the male horns. The horn sheath could be removed in all of the five female, and in eight male skulls, showing a considerable amount of individual variation in length, proportions, and curvature of the horn core in either sex as recorded in table II.

Due to the lesser elevation of the intercornual ridge in the females the angle between the frontal and the occipital planes is more open in the females than in the males, and the total height of the occiput from basion to vertex exceeds the height from basion to lambdoid crest to a less degree in the females than in the males.

In the development of the intercornual ridge and of the frontal surface the adult male skulls vary much among themselves, too. The frontal surface may be convex anteroposteriorly, and the intercornual ridge highest above the core bases, sunken in the median part (Leiden Museum, reg. no. 15384, pl. VI fig. 2), but the frontal also may be markedly concave anteroposteriorly, the intercornual ridge rising into a broad and high prominence in the median line (Leiden Museum, reg. no. 15394, pl. VI fig. 3). The two skulls just referred to, both from the Bartels collection from Java, represent the extremes of variation in these characters found among the male adults. In no. 15384 the height from lambdoid crest to vertex is 60 mm, in no. 15394 this distance is 120 mm, 120 mm being the height from basion to lambdoid crest in both. Thus, the height from basion to lambdoid crest is two-thirds the basion-vertex height in no. 15384, as opposed to only one-half in no. 15394. Broadly speaking, no. 15384 marks an approach to the female banteng skull (see pl. VIII figs. 2-3), while no. 15394 marks an approach to the gaur skull (see Rütimeyer, 1867, pl. II (recent), and Colbert and Hooijer, 1953, pl. 33 (fossil)).

With these important individual and sexual variations in the recent skull of *Bibos javanicus* in mind, let us turn to the fossil skulls of *Bibos* collected in Java by Dubois.

The holotype of *Bibos palaesondaicus* Dubois is a skull from Trinil (Coll. Dub. no. 2798) with both horn cores and the occiput well preserved (pl. VI fig. 1). The frontal surface in front of the horn core bases is badly preserved; the orbits are missing, and even the postorbital constriction can only be approximately given as 235 mm. Supraorbital foramina and grooves cannot be seen. The surface of the frontals is almost flat anteroposteriorly in the median line, and there is an intercornual ridge that is well-marked but only very slightly arched transversely. The horn cores curve outward and downward beyond the frontal plane; their diverging angle is 115°, the maximum angle observed in the recent males of *Bibos javanicus*. The cores are oval in cross section at their bases, the horizontal diameter exceeding the vertical by one-third. The cores diminish quite rapidly in diameters while gently curving upward again. Near the tip (that of the right core is not entire) the cores turn backward on their line of projection; the apical portion is roundish in section and slightly turned inward. The surface of the cores shows longitudinal grooves, most distinct below and behind, indicating a faint counterclockwise torsion for the right core.

In occipital view, above the temporal contraction, there is a triangular raised area formed by the interparietals and the parietals. Although sutures cannot be distinguished in the present specimen the landmarks of the interparietal mentioned in the description of neonatus and young skulls of *Bibos* and of *Epileptobos* (pp. 48-50) do show up clearly; between the ends of the temporal fossae, just above the lambdoid crest, there are shallow depressions on either side of a vertical median elevation (whether they contain foramina the state of preservation does not permit to observe), and in the centre, some 3 cm above the lambdoid crest, there is a small foramen, possibly even two. This foramen marks the top of the interparietal, which is fully in the occipital plane, and, above it, the parietal likewise forms an upward extension of the occiput proper. The angle between the occipital plane (taken over lambdoid or occipital crest and upper border of foramen magnum) and that of the frontal is 70°. Between the raised triangle of interparietal and parietal and the horn core bases the posterior surface of the skull is concave transversely, the parietal forming a median boss, most distinctly seen from above, but it forms no part of the intercornual ridge above it.

The lambdoid crest is rather prominent, overhanging the occiput that is entire but for the tips of the paramastoid processes. The skull base is too imperfect for description or measurement. Measurements and various indices of the present skull are given in table 19.

Apart from its rather larger size, as shown by the width of the frontals at the postorbital constriction, the height of the occiput from basion to lambdoid crest, the length and basal diameters of the horn core, the present Trinil skull does not differ from those of adult males of *Bibos javanicus*; it differs as much from female skulls of the recent species as the male skulls do, and, therefore, there can be no doubt that the present skull is of a male individual.

Coll. Dub. no. 2801, originating from Tegoean (pl. VII figs. 1, 4) is a skull with the frontal surface very well preserved. The right orbital margin is entire, of the left orbit only a small part of the upper rim remains. The naso-frontal notch is seen at the anterior end. Only the left horn core is in place, the pedicle of the right is broken but the right core is preserved separately. Neither of the cores is complete apically.

The naso-frontal notch extends backward as far as the junction of lacrimal and frontal in the upper margin of the orbit. At this level the frontal surface presents a wavy outline from side to side: it is slightly depressed in the median line, but on either side it is convex, then concave in front of the supraorbital grooves, and rises again into the upper rims of the orbits. The diameter of the right orbit is 60 mm; the opening of the supraorbital canal is behind the posterior border of the orbit, which is quite prominent laterally and behind which the frontals narrow to a width of 205 mm. At the level of the postorbital constriction there is a low but well-defined median sagittal ridge on the frontal bones that continues backward into the median prominence of the intercornual ridge. The frontal surface is weakly concave anteroposteriorly; it is also concave transversely on either side of the sagittal ridge, between this ridge and the supraorbital grooves. These supraorbital grooves are distinctly marked; a portion of the left is roofed over by bone. At the level of the anterior bases of the horn cores the grooves are about 15 cm apart, converging anteriorly to a distance of about 10 cm above the orbits; beyond this they fade out. The supraorbital foramina are 11½ cm apart and located on a level with the postorbital constriction.

The skull vertex is marked by a median prominence between the horn core bases; the intercornual ridge is highest in the middle, the two sides sloping outward into the horn core bases forming an angle of 145° at the top. The core is ovate at base, slightly more compressed from above downward than that in the type above described but resembling the latter closely in curvature. The apical third is missing on both sides. The cores diverge at an angle of 120°.

The occipital surface is much more extended above the lambdoid or occipital crest in the present skull than in the type specimen: the distance from lambdoid crest to vertex is not less than 125 mm, above the variation limits found in recent male bantengs (60-120 mm). The distance from basion to lambdoid crest (115 mm), and that from basion to vertex (240 mm) are within recent limits, but the occiput height index (48) is outside the range of variation of this index in recent specimens (50-67).

The two depressions on the nuchal crest, between the ends of the temporal fossae, are visible as well as a median depression just above the intertemporal bridge. The top of the raised triangular area above and including the nuchal crest just fails to reach the skull vertex. This triangle formed by interparietal and parietal stands out from the hinder surface of the skull much more clearly than in any of the recent banteng skulls I have seen (pl. VII fig. 4).

The sides of the occiput are imperfect below the intertemporal contraction, and most of the paramastoid processes is gone. The skull base, beyond the tuberosities on the basioccipital, is severely damaged. In the temporal fossae the sutures of the parietals can be distinguished; the parietal extends forward almost to the pterygoid crest just as it does in recent *Bibos*.

There are several points in which the present specimen differs from recent skulls of male bantengs; those relating to the occipital surface have already been stated. The configuration of the frontal surface also presents marked differences, for in none of the recent skulls does the frontal present a continuous sagittal ridge extending from just behind the nasals to the vertex such as shown in the present fossil skull. The interfrontal suture is either depressed, or level with the frontal surfaces on either side, never marked by a ridge. In addition to this, the surface of the frontals on either side of the median sagittal line is convex or flattened in recent skulls; it is never hollowed between the supraorbital grooves to the extent shown in the fossil skull. The anteroposterior concavity of the frontals, moreover, is more marked in the fossil than in all but one of the recent skulls, viz., no. 15394. In the latter, the prominence of the intercornual ridge is even greater than that in the fossil, the two sloping sides enclosing an angle of 125° (pl. VI fig. 3). Even so, the elevation of the vertex above the occipital crest remains greater in the fossil than in the recent skull, as stated above. This is also shown by the angle between the frontal and the occipital planes, which is 60° in the present fossil as opposed to 65° (the minimum observed among the recent skulls) in no. 15394. The horn cores in the present fossil skull are as large as the largest encountered in the recent series (cat. e and no. 15388), but their diverging angle is wider, viz., 120° against 80°-115° in recent male bantengs.

Coll. Dub. no. 2805, from Nongko near Kedoeng Broeboes, is a rather fragmentary specimen, comprising most of the occiput below the lambdoid crest, the right half of the hinder surface above this crest including the vertex, part of the right horn core and also part of the superior and posterior borders of the right orbit. The specimen offers very little for description; the measurements given in table 19 show that the distance between orbit and base of horn core is rather small, the elevation of the vertex above the occipital crest, however, more marked than in all recent skulls but one (no. 15394).

Coll. Dub. no. 2832 (Pati Ajam) is a fronto-occipital skull portion with the left core (Coll. Dub. no. 2962) attached to it, but the right (Coll. Dub. no. 2964) separately preserved as the pedicle is broken. The orbits are not preserved; the width of the frontals at the postorbital constriction, however, can be given and is the same as that in Coll. Dub. no. 2801. In contradistinction to the latter specimen the frontals are not elevated into a ridge in the sagittal line; in this respect the present skull resembles the type. Supraorbital grooves are not very marked, either. The intercornual ridge is slightly raised in the middle, more so than in the type skull, the two sides meeting at a very open angle (150°). The diverging angle of the horn cores can be approximately given as 100°, less wide than that in the above described specimens (115°-120°); the cores themselves resemble those in Coll. Dub. no. 2798 closely in basal diameters, and their distal halves are gone.

The occiput is rather damaged below the occipital crest but the foramen magnum is entire. Although both in height from basion to lambdoid crest and in basion-vertex height the present skull is smaller than either of those already described it is an intermediate specimen as far as the ratio of these measurements, the occiput height index, is concerned. It should further be noted that there is no conspicuous triangle of interparietal and parietal above the occipital crest such as that in Coll. Dub. no. 2801 in which it is well raised from the hinder skull surface. In the present specimen this structure is barely set off from the surface above the occipital crest, just as it is in most recent skulls. The frontal surface is moderately hollowed anteroposteriorly, but the angle at which it meets the plane of the occiput (60°) is more acute than that in any recent skull of the banteng that has come to my notice.

Coll. Dub. no. 2774 (Trinil) is the back part of a skull, broken off at the orbits, with entire horn cores. Frontal and occipital views are given in pl. VII figs. 2-3. In frontal aspect the present skull is rather like Coll. Dub. no. 2801, showing a low distinct ridge on the interfrontal suture, and presenting a surface that is weakly concave transversely between the sagittal ridge and the supraorbital grooves (the external borders of which are rather prominent in this specimen) but there is a marked difference in the configuration of the intercornual ridge between the two skulls. In Coll. Dub. no. 2774 the intercornual ridge is not raised but sunken in its median part, the bases of the horn cores being more elevated than the central portion of the transverse ridge. On the posterior surface of the intercornual ridge we find the triangle formed by interparietal and parietal of huge dimensions, springing out from the surface of the skull behind for a distance of about 5 cm, and overhanging the portion of the occiput below the lambdoid crest to a marked degree. The parietal boss does not form part of the intercornual ridge; it is placed behind the line connecting the bases of the horn cores, and rises to a greater height, forming the real skull vertex. Posteriorly it has a large depression in the centre, and the nuchal crest at its base shows two transversely elongated depressions, on either side of the median line. No doubt it is this uncommon development at the vertex that induced Dubois to provisionally consider the present skull to represent a new species of *Bibos,* but the name coined by him in manuscript never appeared in print. This would have been pointless, anyway, since the structure above the nuchal crest is merely an extraordinarily well developed interparieto-parietal triangle such as we observe in several other fossil Java skulls, though in none of them it is as prominent and conspicuous as it is in Coll. Dub. no. 2774. It will be recalled that the triangle formed by interparietal and parietal stands out more clearly in some fossil skulls than in the recent, and in the present case this development merely has been carried somewhat to an extreme.

The horn cores, diverging posteriorly at an angle of 120° just as in Coll. Dub. no. 2801, are rather shorter and less curved than those in the type Coll. Dub. no. 2798, but as is readily seen from table II the variation in horn core measurements and indices among recent males of *Bibos javanicus* is so wide indeed that this difference can be accounted for by individual variation within a single species. The unusual development of the parietal boss notwithstanding, the angle formed by the frontal and the occipital planes is 60°, as in Coll. Dub. nos. 2801 and 2832, and the occiput height index as well as the measurements on which it is based are just the same as those in Coll. Dub. no. 2798 (table 19). In occipital width (over the paramastoid processes) the present skull is intermediate, but the condyle width is greater than in the other fossil skulls, representing the maximum found for the recent males.

Comparison between the measurements of the fossil and of the recent skulls of *Bibos* in table 19 further shows that in the fossil specimens the length from nasals to vertex, and the distance between orbit and horn core are to the lower side of the ranges of variation found for these measurements in recent skulls, whereas on the contrary the frontal and occipital widths of the fossil skulls often are to the higher side of, or even above the corresponding recent ranges. The conclusion seems warranted therefore that the skull of *Bibos palaesondaicus* is proportionally wider than that of *Bibos javanicus*.

Coll. Dub. no. 2810, from Kedoeng Broeboes, is a skull portion with the horn cores broken off at base, but with the occipital surface fairly complete otherwise, and the frontal surface intact in the median line to a distance of ca. 15 cm in front of the vertex. This specimen, again, has a frontal surface concave anteroposteriorly, and provided with a ridge on the sagittal (interfrontal) suture not seen in recent skulls. The vertex is not quite on the intercornual ridge but slightly behind, formed by the top of the parietal boss that is such a distinct feature in the preceding specimen. However, the intercornual ridge itself, unlike that in the last specimen, is highest in the middle, and the posterior prominence of the parietal is less marked, although more so than that in Coll. Dub. nos. 2798 and 2801. The height at which the vertex is elevated above the lambdoid crest is 125 mm in the present skull, just as in Coll. Dub. no. 2801. The angle at which the frontal surface is inclined to the occipital plane is only 50°, more acute than that in the other fossil skulls (60°-70°), denoting a more sharply protruding vertex than is found in recent male bantengs (65°-80°). The temporal contraction is very marked. The temporal fossae are exposed along their entire length, showing the parietal to extend forward to 1 cm from the pterygoid crest, the length of the fossa, from this crest to the hinder end, being 13 cm.

Beyond this, there remains nothing to be said about the present skull, but there is an entire and isolated horn core from Kali Gedeh (Coll. Dub. no. 11198) the measurements of which are given in the same column as those of Coll. Dub. no. 2810 in table 19. The horn core, which is of the left side, is the only complete specimen among the isolated *Bibos* horn cores in the Dubois collection, and in shape as well as in size it conforms rather wel with that of Coll. Dub. no. 2798. Like the latter, Coll. Dub. no. 11198 is longer than any recent banteng horn core available.

Coll. Dub. no. 2797 (pl. VI fig. 4, pl. IX fig. 3) is the Tegoean skull on which Dubois based his description of *Bibos protocavifrons*. The specimen carries only one horn core, and lacks the basioccipital and most of the exoccipitals. The orbits are broken away, but most of the frontal surface between and behind the orbits is preserved.

Of the supraorbital grooves that on the right side is best preserved; the distance between the supraorbital foramina is 11 cm. In front of this level, that is, just above the orbits, the frontal surface is weakly convex from side to side and flat anteroposteriorly. Just behind the foramina there emerges a sagittal ridge on the frontals, which become markedly concave anteroposteriorly, curving upward behind into a very thick intercornual ridge. The surface on either side of the median ridge is hollowed transversely; the median ridge fades out again just below the intercornual ridge, which is curved forward at the apex, and rounded off above. The two sides of the intercornual ridge slope away toward the cores, and diverge at an angle of 105°; the slope is decidedly more steep than that in the recent banteng, in which the angle enclosed by the two sloping sides is 125° or greater. The anteroposterior concavity of the frontals, too, is more pronounced than in any of the remaining fossil skulls or in the recent.

The left horn core, the basal half of which is in situ, curves downward and outward just as in the other skulls; it forms an angle of 60° with the median line, and the diverging angle of the cores, therefore, must have been 120°. In basal diameters it is smaller than the cores of the skulls above described, just within recent limits.

In occipital aspect the great elevation of the vertex is striking: the distance between the occipital crest and the vertex is not less than 145 mm, exceeding that in the other fossil Java skulls in which this distance varies from 90 mm (in Coll. Dub. nos. 2798 and 2774) to 125 mm (in Coll. Dub. nos. 2801 and 2810). As the basion is not preserved the total height of the occipital surface cannot be given. The triangle formed by interparietal and parietal is set off from the surface of the skull, but not markedly so. The tip of the triangle remains below the highest median point of the intercornual ridge, as usual. The temporal contraction is intermediate, the brain case width is just the same as that in the few fossil skulls in which this measurement can be taken.

Because of the excessive concavity of the frontals from front to back it is not well possible to determine the frontal plane, and the angle at which it meets the occipital plane. The occipital plane cannot be determined because the upper border of the foramen magnum is missing. In the presence of the powerful and forwardly curving intercornual ridge the present specimen does resemble *Bibos gaurus,* as it does also in the concavity of the frontal region. Yet it does not seem necessary to uphold the species *Bibos protocavifrons* Dubois for this specimen possesses the characters by which other fossil *Bibos* skulls from Java are distinguishable from the recent banteng skulls of the same island, viz., the sagittal ridge on the frontals, the transverse concavity of the surface between this ridge and the supraorbital grooves, the anteroposterior concavity of the frontals, the greater elevation of the intercornual ridge, the more widely diverging horn cores, and the more distinctly marked interparieto-parietal triangle. Of these various distinguishing characters some are more marked in one, others are more marked in another of the series of fossil skulls. In the present specimen it is the third and fourth of the characters listed above that are the most striking to the eye, whereby Coll. Dub.

no. 2797 marks an approach to the gaur. A similar, though less remarkable approach to the gaur skull is sometimes found in the recent banteng also (Leiden Museum, reg. no. 15394). Therefore, my contention is that the present fossil skull is not entitled to a distinct specific name, but may be regarded as an individual variation among the series of fossil skulls of *Bibos* from Java thus far described, all of which referable to male individuals of single species, *Bibos palaesondaicus* Dubois.

Another Tegoean specimen, Coll. Dub. no. 2799, comprises most of the frontal region without, however, the orbits. The basal half of the left horn core only is present, and very little is left of the occiput below the lambdoid crest. The characteristic median sagittal ridge is shown on the frontals, which are only slightly hollowed both transversely and anteroposteriorly. The horn core is more compressed from above downward than in the other skulls, giving a compression index of only 58 (recent range of variation 65-78). The core diverges backward from the median line at an angle of 55°; the resulting diverging angle of 110° is less than in most of the other males. The specimen is further noticeable because of its very prominent interparietals, which project posteriorly well beyond the nuchal crest: the top of the interparietals, marked as usual by a foramen, is 4 cm above the basal foramina on the nuchal crest, and overhangs that crest for a distance of about 3 cm. Further upward, the median ridge formed by the parietal merges rapidly with the surface and does not extend up to the intercornual ridge. The elevation of the vertex above the lambdoid crest is 115 mm. The angle at which the two sides of the intercornual ridge meet at the skull top is 140°.

Coll. Dub. no. 2804 (Kedoeng Broeboes) has the basal parts of both horn cores but lacks the lower portion of the occiput. It is a narrow specimen, the width of the frontals at the postorbital constriction being only 190 mm, although the brain case width is the same as that in wider skulls. The configuration of the frontal surface is like that in most of the other fossil skulls, a sagittal ridge leading up to the vertex, on both sides of which the frontals are hollowed. The anteroposterior concavity of the frontals is only slight. The horn cores diverge posteriorly at an angle of only 105°, the minimum angle found among the fossil males, and they are, moreover, more slender and less compressed dorsoventrally than in any of the above described skulls. However, the elevation of the vertex above the lambdoid crest amounts to 125 mm, which leaves no doubt as to the sex of the individual to which it belonged. The triangle above the nuchal crest is shaped as that in the last specimen, with its greatest posterior prominence at the top of the interparietals, the parietal ridge receding upward into the hinder skull surface. The sides of the intercornual ridge form an angle at the top of 130°.

Coll. Dub. no. 2808 (Pati Ajam) likewise has the basal parts of both horn cores, diverging posteriorly at an angle of 115°. Like the last specimen it is broken off anteriorly at the postorbital constriction and has a distinct ridge on the interfrontal suture. The vertex is about 115 mm above the occipital crest. The temporal contraction is less marked than that in the other fossil males, being 130 mm against only 90-115 mm. It must have exceeded the brain case width, which, however, cannot be exactly measured. The angle formed by the two sloping sides of the intercornual ridge is ca. 135°; the parietal forms a prominent vertical ridge behind, but the vertex is on the intercornual ridge.

Various remaining skull fragments of *Bibos* are too incomplete to add anything of value to our knowledge of the male skull of *Bibos palaesondaicus*. One of these is Coll. Dub. no. 2819 (exact locality unknown) which comprises the upper portion of the frontals and of the occiput, without the horn cores, and which duplicates Coll. Dub. no. 2797 in the presence of a strong and forwardly curved intercornual ridge, although the frontal surface is not hollowed to the same extent as that in the more complete specimen. A similar but somewhat distorted specimen (Coll. Dub. no. 2768) has a very prominent vertex that rises about 120 mm above the lambdoid crest. Coll. Dub. no. 2792 (Kedoeng Broeboes) consists of the occiput without the vertex. The basal depressions of the interparietal just above the lambdoid crest are very marked; at the broken upper edge the median ridge of the parietal has not yet merged with the surface, the edge being 85 mm above the lambdoid crest. Another Kedoeng Broeboes specimen (Coll. Dub. no. 2800), least width of frontals 195 mm, has the vertex at least 110 mm above that crest.

The measurements and indices of the fossil male skulls of *Bibos palaesondaicus* as well as the corresponding ranges of variation found for the males of *Bibos javanicus* are presented in table 19.

In the opinion of Van der Maarel (1932) the fossil male skulls of *Bibos* from Java (Watoealang, Kedoeng Kendang, and Mendoet near Tinggang) described and figured by him are specifically identical with the recent Java banteng. He did notice some differences, such as the occasionally greater development of the horn cores, and the less developed facial crest in the fossil as compared with the recent male skulls of *Bibos javanicus,* but failed to pay attention to the presence of a sagittal ridge on the frontals (shown in the figures), to the diverging angle of the horn cores, or to the angle between frontal and occipital planes. He states that "the relation between height of supra- and infracristal portion of the occiput has but little value" (l.c., p. 44). In these points as well as in others detailed above the fossil male skulls do differ from those of the recent male Java banteng, although the various distinguishing characters do not invariably show in every fossil specimen.

TABLE 19

Measurements of male skulls of *Bibos palaesondaicus*

Coll. Dub. nos.	(type) 2798	2801	2805	2832	2774	2810 11198	2797	2799	2804	2808	*Bibos javanicus* ♂♂
Length from posterior end of nasals to vertex	—	215	—	—	—	—	—	—	—	—	210—250
Length from posterior border of orbit to posterior base of horn core	—	ca. 195	195	—	175	—	—	—	—	—	170—215
Width of occipital condyles	115	115	115	100	120	—	—	—	—	—	100—120
Width of occiput over paramastoid processes	185	180	200	ca. 160	190	165	—	—	—	—	160—200
Least width of occiput between temporal fossae	100	ca. 115	115	90	115	90	110	115	90	130	85—130
Width of frontals at postorbital constriction	ca. 235	205	—	205	225	—	ca. 210	210	190	200	180—210
Width of brain case at middle of temporal fossae	—	115	—	—	—	115	115	—	115	—	110—130
Distance between orbit and base of horn core	—	—	110	—	ca. 115	—	—	—	—	—	105—145
Height of occiput from basion to lambdoid crest	135	115	115	105	135	110	—	—	—	—	105—120
Height from basion to vertex	225	240	230	205	225	235	—	—	—	—	180—240
Occiput height index $\left(\frac{\text{basion-lambdoid cr. x 100}}{\text{basion-vertex}}\right)$	60	48	50	51	60	47	—	—	—	—	50—67
Angle between frontal and occipital planes	70°	60°	—	60°	60°	50°	—	—	—	—	65°—80°
Diverging angle of horn cores	115°	120°	—	ca. 100°	120°	—	120°	110°	105°	115°	80°—115°
Horn core, horizontal diameter at base	115	110	105	115	120	105	100	120	90	ca. 115	85—110
Vertical diameter at right angles to long. axis	85	75	80	85	80	75	75	70	75	80	60—75
Basal circumference of horn core	335	300	305	325	320	295	270	300	360	—	245—295
Core length on inner curve	430	—	—	—	310	420	—	—	—	—	260—385
Idem, outer curve	520	—	—	—	340	530	—	—	—	—	360—530
Straight length from upper base to tip	315	—	—	—	270	310	—	—	—	—	190—300
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	165	—	—	—	126	171	—	—	—	—	146—211
Index of compression $\left(\frac{\text{vert. diam. x 100}}{\text{horizontal diam.}}\right)$	74	68	76	74	67	71	75	58	83	ca. 70	65—78
Index of proportion $\left(\frac{\text{inner curve x 100}}{\text{circumference}}\right)$	128	—	—	—	97	142	—	—	—	—	98—152
Index of length $\left(\frac{\text{inner curve x 100}}{\text{width of frontals}}\right)$	ca. 183	—	—	—	138	—	—	—	—	—	127—211

Van der Maarel did not fail to observe that the skull from Trinil described by Stremme (1911, pp. 137-139, pl. XX figs. 10-11) is different from those described by himself. "Stremme's specimen is — in my opinion — very decidedly distinguished from adult crania of the Javan banting by totally different form and course of the horn-cores" (Van der Maarel, 1932, p. 54). There are skulls resembling that of Stremme's description in the Dubois collection, and these will now be considered.

Coll. Dub. no. 2772, originating from Trinil (pl. VIII fig. 1, pl. IX fig. 4) comprises most of the frontals as well as the entire horn cores and occiput. Part of the right orbit only is preserved. The frontals are slightly raised in the median line without, however, forming a ridge in the sagittal plane, and are flattened anteroposteriorly. Between the bases of the horn cores the surface is much depressed in the median line, making the intercornual ridge markedly concave transversely. The bases of the horn cores are well raised above the median skull vertex, and diverge backward at an angle of only 90°. The cores are but slightly curved, first downward and then upward; seen from above they are almost straight, tapering rapidly and regularly to the tip. The cross section forms an oval, slightly more flattened dorsally than ventrally.

In occipital view it is evident that the vertex is not elevated above the lambdoid crest to a great extent; the intercornual ridge is only 70 mm above the crest in the median line. The nuchal crest, enclosed by the lambdoid crest below and the intertemporal bridge above, is only 70 mm wide transversely between the ends of the temporal fossae, and shows the two foramina on either side of the median line, foramina marking the base of the interparietal, quite clearly. The central foramen that marks the top of the interparietal is placed 2½ cm above the lower foramina, and above it the triangle of the parietal is well marked off from the surface, extending upward just to the vertex of the skull. The lambdoid crest overhangs the occiput, especially in its lateral parts; the angle between the frontal and the occipital planes is just a right angle, 90°.

The present skull in almost all dimensions is smaller than most of the fossil *Bibos* skulls from Java described above as belonging to males of *Bibos palaesondaicus*. The basion-vertex height especially is rather less, even when compared with that of Coll. Dub. no. 2774, which, just as the present skull, has the intercornual ridge sunken in the middle. The horn core of Coll. no. 2772 is less compressed basally than that in all but one of the male skulls (Coll. Dub. no. 2804), and less curved, too. The most important differences, however, are in the angle at which the horn cores diverge backward (90° as opposed to 105°-120°), and the angle between frontal and occipital planes (90° instead of only 50°-70°). Although the Trinil skull described by Stremme is somewhat larger (frontal width below horn cores 222 mm, least width of occiput 95 mm) it agrees with the present skull in the diverging angle of the horn cores, which is about 90° as judged by the figure (Stremme, 1911, pl. XX fig. 11), in the shape of the horn cores, and in the comparatively slight elevation of the vertex above the lambdoid crest. Unfortunately the angle between frontal and occipital planes has not been given by Stremme and cannot be judged from his figures. The height of the occiput is taken from the upper margin of the foramen magnum instead of from the basion, and the "Höhe des oberen Hinterhauptsbeines" recorded as 114 mm is not the height of the supraoccipital proper, and not the interval between foramen magnum and lambdoid crest either (Van der Maarel, 1932, p. 53). However, from the occipital aspect given by Stremme (1911, pl. XX fig. 10) I figure the height from basion to lambdoid crest to have been ca. 120 mm, and the basion-vertex height ca. 200 mm, which gives ca. 80 mm for the elevation of the vertex above the lambdoid crest, a figure lower than that found in the male skulls of *Bibos palaesondaicus* (90-145 mm).

The characters by which the present skull (Coll. Dub. no. 2772) as well as that described by Stremme can be differentiated from those of the males of *Bibos palaesondaicus* are the same as those by which the female skull of *Bibos javanicus* differs from the male skull of the same species. As we have seen on p. 80 the female *Bibos javanicus* skull differs from the male in the lesser basion-vertex height, in the less prominent intercornual ridge, in the more open angle between frontal and occipital planes, and, above all, in the less widely diverging horn cores, which are straighter, shorter, and less compressed basally than those in males.

Since, therefore, Coll. Dub. no. 2772 (and also the skull described by Stremme) differ from the male skull of *Bibos palaesondaicus* in the same points as recent female skulls do the conclusion in inevitable that they represent the female of the fossil banteng, *Bibos palaesondaicus.*

Secondary sexual characters are more marked in the recent Java banteng than they are in *Bibos palaesondaicus,* for the females of the recent Java banteng have very small horn cores, much smaller than those in the females of *Bibos palaesondaicus.* Moreover, they are more distinctly turned backward, diverging posteriorly at angles of 45°-65° only. In the Dubois collection we have some fossil horn cores found near Kedoeng Broeboes (Coll. Dub. nos. 5020 and 10361) resembling those of the recent adult female of the Java banteng, but these isolated specimens belong to immature individuals. Von Koenigswald (1933, p. 94) had already arrived at the conclusion that the males and females of the fossil Java banteng are less markedly differentiated in horn core size than are those of the living Java banteng. In the living Bornean banteng, in which the horns are frequently smaller than those in the Java banteng, and less widely divergent behind (75° in a male skull from Eastern Borneo, Leiden Museum, cat. ost. h), the female is similar in horn development to the female of the Java banteng (see Gans, 1915, pl. II figs. VII-VIII). In the Burma race the horns of cows are relatively long (Lydekker, 1913, p. 28) 1), but in a female from Perak the horns are very short, as in the typical race (Lydekker, l.c., p. 29).

The female skull of *Bibos palaesondaicus* to be considered next is Coll. Dub. no. 2812, likewise from Trinil (pl. VIII fig. 4). This specimen deserves special attention as it was referred by Dubois (1908, p. 1261/62) to a distinct species, *Leptobos dependicornus*. It has since been examined by Pilgrim, who states that it cannot, in his opinion, be referred to *Leptobos*. "It presents characters which are intermediate between *Leptobos* and *Bibos*, and should probably be made type of a new genus" (Pilgrim, 1939, p. 303). The solution of the problem will be found in table 20; Coll. Dub. no. 2812 is so very close to Coll. Dub. no. 2772 in measurements, angles, and indices as to leave no doubt that the former, like the latter, is a female skull of the fossil Java banteng. The orbit is partially preserved on the left side; the supraorbital foramina are 12 cm apart, and placed at the narrowest part of the frontals, which are shaped just as in Coll. Dub. no. 2772. The intercornual ridge is markedly concave transversely; only the basal parts of the horn cores remain, and these diverge backward at slightly less than a right angle. The temporal contraction is more marked, the elevation of the vertex above the lambdoid crest less marked than those in Coll. Dub. no. 2772. The region of the interparietal and parietal is shaped as that in the last specimen, only the apex of the raised triangle does not quite reach up to the vertex. The fronto-parietal sutures are distinct in the present specimen; their median anterior point is just at the vertex, and the two branches diverge at an angle of ca. 105°, curving outward to the posterior inner bases of the horn cores just as in recent female banteng skulls (pl. VIII figs. 2-3) in which the parietal sutures enclose an angle of 90° or less.

Coll. Dub. no. 2809, from Kedoeng Broeboes, is a fronto-occipital skull portion with the left core broken off at base, the right (Coll. Dub. no. 2966) for the most part preserved. The frontals are broken off about 18 cm in front

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1) I can find no base for Von Koenigswald's statement that the horns of the female Bornean banteng are much stronger and longer than those of the female Java banteng unless he worked with incorrectly localized or sexed skulls. Reference should be made to Gans's figures cited above.

of the vertex, but the nasals do not show yet. The orbits are broken, and even the least frontal width cannot be measured. At the level of the postorbital constriction the frontal surface is convex transversely, but there is no median ridge. In anteroposterior direction the frontals are convex from behind the orbits to the vertex. The intercornual ridge is slightly higher in the middle than above the horn core bases, instead of transversely concave as in Coll. Dub. nos. 2772 and 2812. However, the elevation of the vertex is only 70 mm above the lambdoid crest, and the cores diverge backward at an angle of 90°, whereby the present skull is as distinct from those of the males of *Bibos palaesondaicus* as are the two last mentioned specimens. The contraction of the occiput between the ends of the temporal fossae is less marked, the horn cores are greater in horizontal basal diameters than those in the two preceding skulls. Seen from above the right horn core is not straight (as in Coll. Dub. no. 2772) but slightly curved with the concavity forward; it is broken off at a distance of 23 cm from the base along the inner curve, and the broken end measures 65 by 50 mm, slightly more compressed from above downward than the core of Coll. Dub. no. 2772 at the same distance from the base (60 by 50 mm). The apex of the interparieto-parietal triangle is prominent but remains just below the vertex, as in Coll. Dub. no. 2812.

Coll. Dub. no. 2802, again from Kedoeng Broeboes, also has part of the right horn core but nothing of the frontals is preserved in front of the intercornual ridge. This ridge is highest in the middle, although only very slightly so, and is elevated at most 80 mm above the lambdoid crest, which is not very distinctly shown. The horn core is preserved for a length of 14 cm only, appears to diverge backward from the median line at the same angle as that in the last specimen, and also shows a slight forward curve. Due to damage the parietal boss cannot be seen. The width between the temporal fossae is rather great.

In Coll. Dub. no. 2778 (Trinil) the temporal contraction is as marked as that in Coll. Dub. no. 2772; unfortunately the vertex is incomplete. What is left of the intercornual ridge shows that it is either straight or very slightly concave transversely, and elevated at most 50 mm above the lambdoid crest. Although nothing of the horn cores is preserved I have no doubt that the present specimen represents a female.

Coll. Dub. no. 2771 (Trinil) is a poorly preserved specimen, similar to Coll. Dub. nos. 2772 and 2812 in the marked concavity of the intercornual ridge. The parietal boss is more prominent behind; the bases of the horn cores diverge backward at an angle of ca. 90°. The sutures between parietal and frontal can be distinguished, and they indent the frontals behind at an angle of ca. 75°. The slight elevation of the vertex above the lambdoid crest (60 mm) is the same as that in Coll. Dub. no. 2812.

Coll. Dub. no. 2769 (Trinil), weakly concave transversely over the intercornual ridge, lacks the lower portion of the occiput, but in the height of the vertex above the lambdoid crest (ca. 60 mm) it is a characteristically female specimen. The interparieto-parietal triangle stands out from the skull surface above the moderate temporal contraction; it reaches upward just to the vertex. The brain case width is somewhat greater than that in the other fossil skulls. Part of the base of the left horn core is preserved, curving backward as distinctly as it does in other females. The frontal surface is flat as far as preserved, without a median ridge.

Coll. Dub. no. 2823 (Bangle) lacks the horn cores, but enough of the frontals is preserved to determine the angle between the frontal and occipital planes, which is 75°. Moreover, the vertex is only 70 mm above the lambdoid crest. The intercornual ridge is straight across as far as preserved, and there is no sagittal ridge on the frontals.

The measurements of the eight skulls just described above, which I have no doubt belong to females of *Bibos palaesondaicus*, are given in table 20. The corresponding ranges of variation found for the female skulls of *Bibos javanicus* given in the last column of this table indicate that the fossil females exceed the recent in size, and have proportionally much greater horn core dimensions. However, in the comparatively slight elevation of the vertex above the lambdoid crest, the more open angle between frontal and occipital planes, the less backward divergence, and slighter curve of the horn cores the fossil females differ from the fossil males just as the recent females differ from the recent males. For convenience' sake I have put together table 21, in which the differential characters of the two sexes in the fossil and in the recent banteng may be readily seen.

Remaining fronto-occipital skull portions may belong either to male or to female individuals; these specimens are Coll. Dub. no. 517 (locality unknown) holding the base of the right horn core, 95 by 70 mm in diameters, and Coll. Dub. no. 1703 (? Soember Kepoeh), 2780 (Trinil), 2781 (Kebon Doeren), 2783 (Bangle), 2803 (locality unknown), 2807 (Kedoeng Broeboes), 2811 (Kedoeng Broeboes), 2817 (Kedoeng Broeboes), 2822 (locality unknown), 2825 (Soember Kepoeh), 2826 (Bangle), 2828 (Kedoeng Broeboes), and 10554 (Bogo). Horn core fragments including the base are either large: Coll. Dub. nos. 486a (Kedoeng Broeboes) with a horizontal diameter of 115 mm, 2749 (idem), base 110 by 90 mm, and 2834 (locality unknown), base 110 by 80 mm, or they are small, such as Coll. nos. 2958 (Kedoeng Broeboes), base 90 by 65 mm, 2960 (Trinil), base 80 by 65 mm, and 2995 (locality unknown), base 95 by 65 mm. The larger specimens most probably

TABLE 20

Measurements of female skulls of *Bibos palaesondaicus*

Coll. Dub. nos.	2772	2812	2809	2802	2778	2771	2769	2823	*Bibos javanicus* ♀♀
Length from posterior end of nasals to vertex	—	—	180+	—	—	—	—	—	170—200
Length from posterior border of orbit to posterior base of horn core	160	155	—	—	—	—	—	—	150—155
Width of occipital condyles	105	100	105	110	100	100	—	105	90—100
Width of occiput over paramastoid processes	170	170	—	ca. 180	165	—	—	—	150—160
Least width of occiput between temporal fossae	70	60	105	120	ca. 70	ca. 75	90	95	60—80
Width of frontals at postorbital constriction	215	200	—	—	—	—	—	—	150—160
Width of brain case at middle of temporal fossae	115	115	—	—	115	—	120	115	100—120
Distance between orbit and base of horn core	95	95	—	—	—	—	—	—	100—120
Height of occiput from basion to lambdoid crest	110	110	115	ca. 115	120	105	—	115	105—110
Height from basion to vertex	180	170	185	195	ca. 170	165	—	185	155—160
Occiput height index $\left(\frac{\text{basion-lambdoid cr. x 100}}{\text{basion-vertex}}\right)$	61	65	62	ca. 59	ca. 71	66	—	62	66—69
Angle between frontal and occipital planes	90°	85°	80°	—	—	—	—	75°	80°
Diverging angle of horn cores	90°	85°	90°	—	—	ca. 90°	—	—	45°—65°
Horn core, horizontal diameter at base	95	90	115	ca. 100	—	—	—	—	40—60
Vertical diameter at right angles to long. axis	75	70	75	70	—	—	—	—	30—45
Basal circumference of horn core	280	260	310	—	—	—	—	—	110—165
Core length on inner curve	340	—	—	—	—	—	—	—	90—160
Idem, outer curve	360	—	—	—	—	—	—	—	115—200
Straight length from upper base to tip	310	—	—	—	—	—	—	—	80—160
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	116	—	—	—	—	—	—	—	120—144
Index of compression $\left(\frac{\text{vert. diam. x 100}}{\text{horizontal diam.}}\right)$	79	78	65	ca. 70	—	—	—	—	75—89
Index of proportion $\left(\frac{\text{inner curve x 100}}{\text{circumference}}\right)$	121	—	—	—	—	—	—	—	78—97
Index of length $\left(\frac{\text{inner curve x 100}}{\text{width of frontals}}\right)$	158	—	—	—	—	—	—	—	60—100

belonged to males. In the Cosijn collection from the Djetis deposits North of Djetis and Perning, Eastern Java, preserved in the Geological Museum at Leiden, there are two horn core fragments (nos. 27811 and 28136) referable to the present species. Many similar fragments, all without the base, are in the Dubois collection. Since most of these are without a record for the exact locality it is of no use to list them.

TABLE 21

Main differential characters of females and males of recent and fossil *Bibos* of Java

	♀♀	♂♂
Basion-vertex height, recent	155—160	180—240
Idem, fossil	165—195	205—240
Occiput height index, recent	66—69	50—67
Idem, fossil	ca. 59—ca. 71	47—60
Angle between frontal and occiput, recent	80°	65°—80°
Idem, fossil	75°—90°	50°—70°
Diverging angle of horn cores, recent	45°—65°	80°—115°
Idem, fossil	85°—90°	ca. 100°—120°
Horn core curvature index, recent	120—144	146—211
Idem, fossil	116	126—171

As Chasen (1940, p. 205) puts it, there is no evidence for supposing that the typical banteng occurs in a truly wild state anywhere except on the main island of Java. It is probable that *Bibos palaesondaicus* Dubois should be regarded as the immediate ancestor of *Bibos javanicus* (d'Alton); the main steps involved in the transformation from the Pleistocene to the recent animals are those shown in table 21.

The mandibular rami of *Bibos palaesondaicus* agree closely with those of recent *Bibos javanicus*; the most complete specimen, from Trinil (Coll. Dub. no. 336, pl. V fig. 2) is within recent limits of variation in dimensions except for the height behind M3 (table 22).

TABLE 22

Measurements of the mandible of *Bibos palaesondaicus* and of *Bibos javanicus* from Java

	Bibos palaesondaicus Coll. Dub. no. 336	*Bibos javanicus* recent, Java
Length of ramus from mental foramen to hinder surface of angle	330	300—340
Length P3-M3	125	125—135
Height of ascending ramus from lower surface of angle to mandibular notch	155	140—160
Height of ramus behind M3	80	65—75

Coll. Dub. no. 336 lacks the anterior premolar, P_2, which is the most diagnostic tooth, easily distinguishable from its homologue in *Bubalus* (above, p. 73). As the other lower premolars and the molars of *Bibos* do not differ in structure from those of *Bubalus* (Colbert and Hooijer, 1953, pp. 118-120) it is possible to identify only those ramus fragments that have P_2 in place. There are four such specimens in which the P_2 agrees structurally with that of the banteng, viz., Coll. Dub. no. 345 (Trinil, pl. V fig. 4), and Coll. Dub. nos. 2639, 4361, and 8487, all from Trinil. In all of these the length of P_2 is 14 mm, and the width 11 mm, except in Coll. Dub. no. 8487 in which P_2 measures 14 by 9 mm. The last-mentioned specimen is within the limits of the recent and subfossil specimens of P_2 of *Bibos javanicus* (below, p. 99); the P_2 in Coll. Dub. nos. 345, 2639, and 4361 are wider. The length P_3-M_3 in Coll. Dub. no. 345 is 140 mm, greater than that in any of the recent Java bantengs.

In a small collection of fossils from Ngeboeng near Sangiran, Java, presented by Mr. H. R. van Heekeren in January, 1957, there is a perfect and unrolled right P_2 indistinguishable from that of *Bibos palaesondaicus*; the crown is 14 mm long and 10.5 mm wide. The Ngeboeng fossils are of interest as they have been found in association with Sangiran flakes. The material occurs in the upper gravel of the Notopuro Beds; notwithstanding the claims of Van der Hoop, Zeuner, and Von Koenigswald (see Movius, 1955, p. 529) no Trinil fossils have ever before been found in direct and undisputed association with the Sangiran flakes. Since *Bibos palaesondaicus* occurs both in the Trinil and in the Ngandong fauna the present specimen is of no help in determining the age of the Sangiran culture.

The postcranial remains of *Bibos* have already been dealt with in the chapter on *Bubalus palaeokerabau.*

Bibos javanicus (d'Alton) subsp.

As related in the preceding chapter the Pleistocene *Bibos palaesondaicus* Dubois is probably directly ancestral to the living banteng of Java. The recent banteng is generally known in zoological literature as *Bos sondaicus* or *Bos banteng,* but its valid name is *Bibos javanicus* (d'Alton), 1823 (Hooijer, 1956a). This species is known from Burma, Siam, Indo-China and Malaya; in the Malay Archipelago it has been found only in Borneo, Java, and (as a domestic animal) in Bali and Lombok. The absence of the banteng from Sumatra, whence no authentic recent specimen has ever been obtained (Snelleman, 1887, p. 26), is one of the zoogeographical puzzles facing the student of the extant fauna. In the opinion of De Beaufort (1926, p. 62) the banteng has probably lived in Sumatra in former times and has become extinct; fossil remains in proof of this suggestion have not been found in Sumatra as yet, however [1]).

In the Dubois collection from limestone caves in Central Sumatra made in the years 1888 to 1890 there are a number of isolated teeth of large bovines. The cave fauna contains only living species; as far as known the cave forms are at most subspecifically distinct from those living today in Sumatra and/or Java. Usually they are slightly larger than the recent forms (Hooijer, 1949).

Among the isolated large bovine teeth from the Sumatran caves there are nine specimens of the anterior lower premolar, P_2. Eight out of these prove that the banteng was indigenous in Sumatra during the time the cave deposit was formed, for they are indistinguishable from those of the modern *Bibos javanicus*. These specimens are Coll. Dub. nos. 742 a and b, both P_2 dext. from the Lida Ajer cave, Central Sumatra (pl. IX figs. 5-10), Coll. Dub. nos. 809 a and 882 a, both P_2 dext. from the Sibrambang cave, and Coll. Dub. nos. 809 b, 809A a, 882 b, and 882 c, all P_2 sin. from the Sibrambang cave, Central Sumatra. The two Lida Ajer specimens are well preserved and unworn; the likewise unworn P_2 dext. of the holotype of *Bibos javanicus* (Leiden Museum, cat. ost. a) is figured on the same plate for easy comparison. Seven recent P_2s of *Bibos javanicus* vary in crown length from 12 to 14 mm, and in crown width from 8.5 to 9 mm. The subfossil cave P_2s vary in length from 11 to 14.5 mm, and in width from 9 to 10.5 mm. Apart from this tendency to greater width of the crown in the cave P_2s there is nothing by which they can be distinguished from their recent counterparts from Java.

The banteng was an aboriginally wild form in Sumatra in the early Holocene, and its extinction in the island, therefore, is of comparatively recent date. Whether or not the subfossil Sumatran banteng is entitled to subspecific distinction from the modern Java banteng cannot be decided at present.

Subfamily CAPRINAE Gill

Genus CAPRICORNIS Ogilby

Capricornis sumatraensis (Bechstein) subsp.

Capricornis sumatraensis (Bechstein) subsp., the serow or kambing utan, is represented in the Central Sumatran cave collection by a considerable number of teeth, mostly isolated molars, the roots of which have been gnawed

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1) In the recent "Traité de Zoologie" we read that the banteng occurs in the Greater Sunda Islands "à l'exclusion de Sumatra où il n'est connu qu'à l'état fossile..." (Frechkop, 1955, p. 625). The origin of this statement is obscure; there are no fossil remains of the banteng from Sumatra, but only the subfossil cave remains discussed in the present chapter, first referred to in a paper read by me in Paris in 1957 (Hooijer, 1958).

off by porcupines. Not a single bone fragment is preserved. There are a number of recent skulls of the Sumatran serow, *Capricornis sumatraensis sumatraensis* (Bechstein), in the Leiden Museum, and these have been used for comparison with the subfossil cave material.

The teeth of the recent skulls vary only slightly in size among themselves. Both males and females are in the series; there does not appear to be any difference in size of the teeth between the sexes. Apart from the absence of the right P_2 in a single specimen (Leiden Museum, reg. no. 4910) numerical variations of the teeth have not been noticed.

The teeth of *Capricornis* are characterized by their very hypsodont crowns; the bases of the molar crowns are not exposed in the recent skulls available to me except, in some old specimens, those of M^1 and of M_1. The P_4 has the anterior valley closed on the lingual side; there is a complete inner wall to the anterior fossette. In P_3 the anterior valley is open internally in most cases, an exception being Leiden Museum, reg. no. 4911 in which the inner cusp of P_3 is expanded anteriorly and fused at the base to the anterior inner cusp so as to make an isolated anterior fossette. The molars are further characterized by the absence of basal pillars at the inner side of the upper and at the outer side of the lower molars; there are only very few cases in which basal pillars can be observed. Schlosser (1903, p. 169, under *"Nemorrhaedus"*) notes that basal pillars occur in M_1 at most, but it is only in the first molars that the base, and thereby the basal pillar, may be exposed in a skull. Among the collection of isolated *Capricornis* molars from the limestone caves of Central Sumatra there are several instances of last upper molars that possess a definite though slender median basal pillar. These cases will be noted below.

A basal pillar occurs regularly in the posterior outer valley of DM_4 (Leiden Museum, reg. nos. 407 and 5677), not represented in the cave collection.

In both the upper and the lower molar crowns of *Capricornis* the transverse diameters increase from top to base. The anteroposterior diameters of the molar crowns invariably decrease from top to base except in M^3 and in M_3, in which the basal anteroposterior diameter may also be equal to, or even greater than that at the top due to the varying basal prominence of the posterior outer pillar (M^3) or of the third lobe (M_3). Since the bases of the crowns of the recent molars cannot be exposed without breaking away the bone of the jaw the measurements of the teeth have been taken about 1 cm below the occlusal surface, that is, approximately at the level of the alveolar border. The subfossil teeth have been measured in the same manner. Although a certain amount of variation with wear is involved in the measurements thus obtained it is considered legitimate to use these measurements for

TABLE 23

Measurements of the teeth of *Capricornis sumatraensis sumatraensis*

Leiden Museum	cat. a	cat. b	cat. c	cat. h	reg. no. 991	reg. no. 991	reg.no. 1128	reg. no. 4910	reg. no. 4911	reg. no. 5674	reg. no. 5675	reg. no. 5676	reg. no. 5677
	♀	♂	—	—	♂	♀	—	—	♂	♀	—	—	—
P^4, anteroposterior	10	11	10	11	10	11	10	10	10	12	—	—	—
transverse	12	10	12	12	12	11	13	12	11	11	—	—	—
M^1, anteroposterior	14	15	15	14	14	16	13	12	14	15	—	—	—
transverse	14	13	13	14	13	14	16	14	14	12	—	—	—
M^2, anteroposterior	17	17	17	18	17	17	17	15	16	18	—	—	—
transverse	15	13	13	13	14	12	16	14	13	12	—	—	—
M^3, anteroposterior	20	17	18	19	18	18	18	17	17	18	—	—	—
transverse	14	11	12	12	13	11	15	13	12	11	—	—	—
Length M^{1-3}	52	48	48	50	50	50	48	45	49	49	—	—	—
P_4, anteroposterior	12	13	14	12	14	14	14	12	13	14	14	14	—
transverse	8	8	8	8	8	8	8	8	8	8	8	9	—
M_1, anteroposterior	14	15	14	14	15	16	14	12	13	15	15	14	16
transverse	9	9	9	10	10	10	10	9	9	9	10	10	10
M_2, anteroposterior	17	17	17	17	17	17	16	16	16	17	16	17	18
transverse	11	10	9	10	11	11	11	10	10	9	11	10	10
M_3, anteroposterior	25	22	23	23	24	23	24	22	22	22	21	19	—
transverse	11	10	9	10	11	9	10	10	10	9	10	10	—
Length P_3-M_3	81	76	81	77	82	81	78	73	78	78	78	77	—
Length M_{1-3}	56	53	54	53	56	56	54	51	53	54	52	51	—

comparison between the recent and the subfossil teeth because both the recent and the subfossil teeth are represented by rather long series of specimens in varying degrees of wear. If there is no difference in size between the recent teeth and their subfossil homologues the averages of both series would come out approximately the same. As will follow from the tables of measurements below the average dimensions of the teeth in the recent and in the subfossil series are not the same: the subfossil teeth invariably average larger than the corresponding recent .

The material of *Capricornis* from the Sumatran caves is as follows:
Coll. Dub. no. 686a (cave not specified), M^3 sin.
Coll. Dub. no. 738a (Sibrambang cave), M_3 sin.
Coll. Dub. no. 753a (Lida Ajer cave), M^3 dext.
Coll. Dub. no. 754 (cave not specified), 2 upper P, 27 upper and 28 lower M.
Coll. Dub. no. 755 (idem), 1 upper P, 3 upper and 1 lower M.
Coll. Dub. no. 808 (idem), 1 upper P, 16 upper M, 1 lower P, 24 lower M.
Coll. Dub. no. 825 (idem), incomplete M_3 dext.
Coll. Dub. no. 832 (idem), 14 upper M, 3 lower P, 9 lower M.
Coll. Dub. no. 839a (Sibrambang cave), upper P.
Coll. Dub. no. 866 (cave not specified), 3 lower M.
Coll. Dub. no. 867 (idem), 13 upper M, 12 lower M.
Coll. Dub. no. 899a (Djamboe cave), M_3 sin.
Coll. Dub. no. 903 (cave not specified), 2 upper P, 1 upper and 1 lower M.
Coll. Dub. no. 922 (idem), 3 upper M.
Coll. Dub. no. 923 (idem), 3 upper M, 1 lower P, 3 lower M.
Coll. Dub. no. 924 (idem), 1 upper M, 1 lower P, 2 lower M.
Coll. Dub. no. 935b (idem), lower M.
Coll. Dub. no. 959 (Djamboe cave), 1 upper P, 4 upper M, 2 lower P, 4 lower M. .
Coll. Dub. no. 961 (Sibrambang cave), 5 upper M.
Coll. Dub. no. 972 (cave not specified), 2 upper M.
Coll. Dub. no. 975 (Sibrambang cave), 3 upper M, 1 lower P, 2 lower M.
Coll. Dub. no. 1014 (cave not specified), 1 lower P, 1 lower M.
Coll. Dub. no. 1034a (idem), M_3 dext.
Coll. Dub. no. 1102 (idem), 1 upper P, 2 upper M, 1 lower P, 4 lower M.
Coll. Dub. no. 1136 (idem), 1 upper M, 1 lower P, 1 lower M.
Coll. Dub. no. 6996 (idem), 2 lower M.
Coll. Dub. no. 6997 (idem), 6 upper M, 1 lower P, 2 lower M.
Coll. Dub. no. 6999 (idem), 1 upper M, 4 lower M.
Coll. Dub. no. 9985 (Djamboe and Sibrambang caves), M_3 sin.
Coll. Dub. no. 10006 (idem), 1 upper and 1 lower M.
Coll. Dub. no. 10009 (idem), 4 upper P, 2 upper M, 4 lower P, 3 lower M.

TABLE 24

Measurements of subfossil P⁴ of *Capricornis sumatraensis*

Coll Dub. nos.	754a	754b	755a	808d	839a	903a	959m	1102j
Anteroposterior	12	12	11	12	13	12	11	12
Transverse	12	14	14	11	11	13	12	11
Coll. Dub. nos.	10009b	10009d	10009i					
Anteroposterior	12	12	10					
Transverse	13	12	11					

TABLE 25

Measurements of subfossil M¹ of *Capricornis sumatraensis*

Coll. Dub. nos.	754c	754d	754e	754f	754g	755b	808h	832a
Anteroposterior	17	18	19	19	19	16	17	19
Transverse	13	14	14	18	16	12	16	16
Coll. Dub. nos.	832b	832c	832d	867a	903c	922b	923f	1102g
Anteroposterior	18	18	16	18	17	19	17	18
Transverse	15	16	13	16	—	15	15	15

TABLE 26

Measurements of subfossil M² of *Capricornis sumatraensis*

Coll. Dub. nos.	754h	754i	754j	754k	755c	808i	808j	808k
Anteroposterior	20	18	19	20	20	19	19	19
Transverse	16	15	17	19	17	16	16	15
Coll. Dub. nos.	808l	808m	832e	832f	867b	922c	923c	924f
Anteroposterior	19	18	20	21	19	20	19	20
Transverse	16	17	16	18	18	18	14	14
Coll.Dub.nos.	972a	1102f	10006a					
Anteroposterior	20	21	20					
Transverse	16	14	16					

TABLE 27

Measurements of subfossil M³ of *Capricornis sumatraensis*

Coll. Dub. nos.	686a	753a	754l	754m	754n	754o	754p	755d
Anteroposterior	22	21	22	21	21	20	20	21
Transverse	17	16	15	15	16	16	17	16
Coll. Dub. nos.	808a	808b	808c	808e	808f	808g	832g	832h
Anteroposterior	22	21	21	21	20	20	20	22
Transverse	16	17	15	15	14	14	14	15
Coll. Dub. nos.	832i	832j	832k	832l	867d	867e	867f	867g
Anteroposterior	23	22	21	21	23	20	20	22
Transverse	16	17	16	16	15	14	15	16
Coll. Dub. nos.	867h	867i	867j	867k	867l	867m	922a	923a
Anteroposterior	20	22	20	22	22	22	21	20
Transverse	16	15	15	16	15	17	16	15
Coll. Dub. nos.	961r	975e	6997d	6997g				
Anteroposterior	20	21	21	21				
Transverse	16	17	15	15				

TABLE 28

Measurements of subfossil P_4 of *Capricornis sumatraensis*

Coll. Dub. nos.	808n	832m	832n	832o	923g	924g	959k	959l
Anteroposterior	16	14	15	16	14	15	—	14
Transverse	10	9	9	9	8	8	10	9
Coll. Dub. nos.	975f	1014a	1102h	1136a	6997m		10009f	10009l
Anteroposterior	14	15	16	17	16		15	15
Transverse	9	9	10	9	10		9	9
Coll. Dub. nos.	10009n							
Anteroposterior	14							
Transverse	8							

TABLE 29

Measurements of subfossil M_1 of *Capricornis sumatraensis*

Coll. Dub. nos.	754q	754r	754s	754t	808o	808p	808q	866ac
Anteroposterior	18	18	18	19	19	19	17	16
Transverse	11	12	12	11	11	12	10	10
Coll. Dub. nos.	867n	867o	867p	867q	867r	923b	923e	924e
Anteroposterior	17	18	18	16	17	16	17	18
Transverse	13	11	11	11	11	10	10	11
Coll. Dub. nos.	975b	1136c	6996b	10009a				
Anteroposterior	18	16	18	15				
Transverse	10	10	10	10				

TABLE 30

Measurements of subfossil M_2 of *Capricornis sumatraensis*

Coll. Dub. nos.	754u	754v	754w	754x	754y	754z	808r	808s
Anteroposterior	20	19	20	20	21	21	20	20
Tranverse	12	12	13	12	13	11	12	12
Coll. Dub. nos.	808t	808u	808v	832p	832q	866ad	866ae	867s
Anteroposterior	21	20	18	20	20	19	20	20
Transverse	12	12	11	13	11	11	12	11
Coll. Dub. nos.	867t	867u	867v	935b	1014b	1136b	6996a	
Anteroposterior	19	21	19	20	18	20	19	
Transverse	12	11	12	12	12	14	12	
Coll. Dub. nos.	6997h	6999d	10006b					
Anteroposterior	20	20	20					
Transverse	11	12	12					

Several specimens of M^3 in the cave collection possess basal pillars; these specimens are Coll. Dub. no. 808 a, an M^3 dext., with a slender median pillar that has a height of 13 mm, Coll. Dub. no. 808b, an M^3 dext. with a basal pillar 11 mm high, and Coll. Dub. no. 6997d, an M^3 dext. in which the median basal pillar is 11 mm high (pl. III fig. 2). There is also an M^1 dext. (Coll. Dub. no. 1102g) with a median basal pillar that is, however, only 3 mm high. One of the lower molars, Coll. Dub. no. 975b, an M_1 dext., has an external

TABLE 31

Measurements of subfossil M_3 of *Capricornis sumatraensis*

Coll. Dub. nos.	738a	754aa	754ab	754ac	754ad	754ae	754af	
Anteroposterior	26	26	26	26	28	27	28	
Transverse	12	10	10	11	12	12	12	
Coll. Dub. nos.	754ag	754ah	755e	808w	808x	808y	808z	808aa
Anteroposterior	27	27	27	26	24	27	23	25
Transverse	11	12	11	12	11	10	10	11
Coll. Dub. nos.	808ab	832r	832s	867c	867w	867x	899a	923d
Anteroposterior	27	27	27	26	26	27	26	25
Transverse	12	12	12	10	11	11	11	12
Coll. Dub. nos.	924d	959h	959i	959j	1034a	1102e	6997f	
Anteroposterior	24	24	27	24	27	27	28	
Transverse	10	10	12	10	11	11	12	
Coll. Dub. nos.	6999a	6999b						
Anteroposterior	26	25						
Transverse	11	10						

basal pillar about 5 mm high. In none of the remaining isolated cave molars median basal pillars have been observed. Several upper molars have a basal pillar attached to the anterior inner cusp: Coll. Dub. nos. 754f (M^4 sin), 755c (M^2 dext.), and 832i (M^3 dext.). The anterior inner pillar of Coll. Dub. no. 755c is well developed, about 4 mm in diameter, and at least 10 mm high (pl. III fig. 1). Such extra pillars have not been found in the recent molars available for comparison.

The variation ranges and means of the dimensions of the teeth of *Capricornis sumatraensis* presented in table 32 show that the subfossil teeth are

TABLE 32

Variation ranges and means of dimensions of recent and subfossil teeth of *Capricornis sumatraensis*

		Recent		Subfossil	
		Range	Mean	Range	Mean
P^4,	anteroposterior	10—12	11	10—13	12
	transverse	10—13	12	11—14	12
M^1,	anteroposterior	12—16	14	16—19	18
	transverse	12—16	14	12—18	15
M^2,	anteroposterior	15—18	17	18—21	20
	transverse	12—16	14	14—19	16
M^3,	anteroposterior	17—20	18	20—23	21
	transverse	11—15	12	14—17	16
P_4,	anteroposterior	12—14	13	14—17	15
	transverse	8—9	8	8—10	9
M_1,	anteroposterior	12—16	14	15—19	17
	transverse	9—10	10	10—13	11
M_2,	anteroposterior	16—18	17	18—21	20
	transverse	9—11	10	11—14	12
M_3,	anteroposterior	19—25	23	23—28	26
	transverse	9—11	10	10—12	11

larger, on an average, than the recent. In seven out of the sixteen measurements compared the ranges of the recent and of the subfossil teeth do not even overlap. It is clear that the subfossil cave form of *Capricornis sumatraensis* had teeth larger than those of the living Sumatran race.

This result is in harmony with those of previous studies on various subfossil Sumatran cave forms such as orang-utan, porcupine, tiger, Malay tapir, Javan, and Sumatran rhinoceroses (summarized in Hooijer, 1949), in which it was found as a rule that the cave teeth average larger than their recent homologues. In all of these forms there has been a reduction in tooth size since the time of the deposition of the cave remains. The cave fauna does not contain extinct species, and there can be no doubt that the large forms contained in the subfossil fauna are directly ancestral to those now living in Sumatra.

A large extinct subspecies of *Capricornis sumatraensis* from the Middle Pleistocene of Szechwan, China, was described some years ago as *Capricornis sumatraensis kanjereus* Colbert et Hooijer (1953, p. 127). The teeth of this form are at least as large as, or even larger than those of the subfossil Sumatran cave form recorded above; the length of M_3 in two mandibular rami figured (Colbert and Hooijer, 1953, pl. 39) is 27-28 mm, that of M_2, 20-21 mm, and that of P_4, 16-17 mm. These figures are to the higher side of the ranges of variation of these measurements in the subfossil Sumatran form. The length M^{1-3} in the Chinese Pleistocene form is 58-61 mm against only 45-52 mm in the living Sumatran race; that of the Sumatran cave form cannot be given exactly as all the teeth found are isolated specimens, but the length M^{1-3} in the cave form certainly would exceed that in the living Sumatran race to a similar degree.

The Sumatran cave form clearly is not subspecifically the same as the living Sumatran *Capricornis sumatraensis sumatraensis*. In the size of its teeth it is very close to *C. s. kanjereus* from the Middle Pleistocene of China. Although I do not consider the Sumatran cave form to be identical with that of the Chinese Pleistocene either it seems best for the present to leave the large Sumatran cave form subspecifically unnamed until such time as we shall have the materials to establish its distinctness beyond any doubt.

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TABLE I

Measurements of the skulls of *Duboisia*, *Boselaphus*, and *Tetracerus*

																			Boselaphus tragocamelus, Leiden Museum					*Tetracerus quadricornis*, British Mus.	
Coll. Dub. nos.	2037	2038	2039	2041	2042	2043	2044	2045	2046	2047	2048	2049	2050	2051	2071	2072	2073	2075	cat. b	cat. c	no. 2133	no. 2319	no. 9933	43.1.12.86	2.8.14.3
Median length from nasal to occipital crest	—	156	158	168	—	—	—	—	—	—	—	—	—	—	—	—	—	—	235	220	238	218	217	115	120
From a point level with posterior base of horn core to occipital crest	60	59	55	56	—	—	—	59	—	—	—	—	—	—	—	ca. 60	56	—	100	90	96	90	95	46	54
Width at posterior borders of orbits	—	99	97	—	—	—	—	—	105	—	—	98	95	—	95	—	—	—	144	148	155	142	151	78	84
Postorbital constriction	90	91	90	—	ca. 85	92	92	—	89	87	99	89	85	88	86	—	—	90	126	129	132	118	135	65	66
Width of brain case	71	69	65	69	—	—	—	64	—	—	—	—	—	—	—	—	—	—	90	82	88	83	83	56	59
Least distance between parietal crests	30	28	27	ca. 25	—	—	—	30	—	—	—	—	—	—	—	—	28	—	37	28	45	26	36	11	18
Greatest width of occiput	104	—	ca. 100	ca. 105	—	—	—	95	—	—	—	—	—	—	—	ca. 105	95	—	117	—	121	112	118	56	59
Width over paramastoid processes	85	—	75	82	—	—	—	75	—	—	—	—	—	—	—	ca. 78	74	—	106	—	104	100	101	49	50
Height from basion to summit of occipital crest	58	—	55	59	—	—	—	53	—	—	—	—	—	—	—	—	—	—	81	—	87	80	82	40	41
Occiput index $\left(\frac{\text{height x 100}}{\text{paramastoid width}}\right)$	68	—	73	72	—	—	—	71	—	—	—	—	—	—	—	—	—	—	76	—	83	80	81	82	82
Width of occipital condyles	54	—	47	55	—	—	—	48	—	—	—	—	—	—	—	ca. 47	—	—	70	—	69	65	66	32	35
Horn core, length along outer curve	115	75	105	—	ca. 70	—	110	85	100	110	130	115	110	105	—	—	—	105	115	120	105	115	115	50[1]	70
Straight length from outer base to tip	95	65	90	—	ca. 65	—	95	80	85	95	110	95	95	90	—	—	—	95	115	115	100	115	110	50	70
Greatest transverse diameter	36	29	39	35	30	35	32	31	36	32	43	35	38	33	32	33	38	31	47	42	40	41	40	14	13
Vertical diameter at base	19	16	20	25	16	22	18	16	23	20	26	18	22	19	18	21	20	17	35	31	36	33	33	12	14
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	120	115	115	—	—	—	115	105	115	115	120	120	115	115	—	—	—	110	100	105	105	100	105	100	100
Index of compression $\left(\frac{\text{vert. diam. x 100}}{\text{transv. diam.}}\right)$	53	55	51	71	53	63	56	52	64	63	60	51	58	58	56	64	53	55	74	74	90	80	83	86	108
Maximum span of horn cores	172	138	—	—	137	159	—	147	149	144	183	134	144	153	—	—	—	—	175	146	149	141	188	—	—
Interval between horn core tips	150	133	—	—	132	—	—	136	137	118	152	104	—	140	—	—	—	—	170	125	125	114	186	—	—
Angle between preorbital plane of frontal and fronto-parietal plane	—	—	125°	125°	—	—	—	—	—	—	130°	—	130°	—	—	—	—	—	170°	170°	175°	170°	170°	150°	150°
Angle between parietal and occipital planes	100°	—	105°	105°	—	—	—	100°	—	—	—	—	—	—	—	—	—	—	70°	—	70°	75°	80°	ca. 95°	ca. 100°

Coll. Dub. nos	1666	2040	2052a	2054b	2054c	2060a	2061b	2061d	2061e	2061g	2064d	2069a	2069b	2069e	2070a	2074	2208	2506a	2513	2521	6879	6911	8894
Horn core, length along outer curve	125	—	—	—	—	120	—	90	90	—	—	—	—	—	—	—	60	65	—	—	—	—	—
Straight length from outer base to tip	100	—	—	—	—	105	—	80	80	—	—	—	—	—	—	—	55	60	—	—	—	—	—
Greatest transverse diameter	38	37	36	34	34	38	36	29	33	32	42	44	40	43	46	33	23	27	23	31	27	36	39
Vertical diameter at base	22	21	22	19	20	24	22	17	21	17	21	29	26	26	29	20	15	16	16	18	14	19	20
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	125	—	—	—	—	115	—	110	110	—	—	—	—	—	—	—	110	110	—	—	—	—	—
Index of compression $\left(\frac{\text{vert. diam. x 100}}{\text{transv. diam.}}\right)$	58	57	61	56	59	63	61	58	64	53	50	66	65	60	63	61	65	59	70	58	52	53	51

[1] Horn core of Leiden Museum, cat. a.

TABLE II

Measurements of the skull of *Bibos javanicus*

Leiden Museum	(type) cat. a	cat.e	no. 4899	no. 8834	no. 15392	no. 15393	no. 15398	no. 15384	no. 15394	no. 15391	no. 15396	no. 15387	no. 15390	no. 15381	no. 15397	no. 15383	no. 15395	no. 15382	no. 15385	no. 15399	no. 15389	no. 15386	no. 15388	no. 4900a	no. 4900b	no. 1587	♀ cat. b	♀ cat. c	♀ no. 1587	♀ no. 2678	♀ no. 15400
Length from posterior end of nasals to vertex	240	250	215	220	230	240	220	235	210	215	220	230	225	240	220	240	225	240	250	230	225	240	230	215	230	220	195	185	170	175	200
Length from basion to lateral post-palatal notches	185	205	185	190	190	185	180	180	190	170	170	185	185	185	175	195	180	175	190	180	185	185	—	—	—	—	165	160	—	—	155
Length from posterior border of orbit to posterior base of horn core	185	205	170	190	210	205	200	200	215	195	190	185	200	195	180	210	185	190	190	195	195	210	210	—	200	190	155	150	150	—	150
Width of occipital condyles	105	115	110	105	115	105	100	110	110	105	105	110	120	115	100	110	110	115	120	110	110	110	—	—	—	—	95	100	—	—	90
Width of occiput over paramastoid processes	170	200	175	185	180	165	170	170	170	165	170	190	185	185	160	185	170	170	190	185	185	185	—	—	—	—	150	160	—	—	150
Least width of occiput between temporal fossae	105	90	95	90	125	125	95	120	110	105	90	115	125	95	95	130	105	95	125	85	105	120	—	—	100	105	75	80	80	70	60
Width of frontals at postorbital constriction	180	210	190	185	195	205	185	200	200	185	185	195	200	190	180	205	200	210	205	190	200	205	205	205	190	200	160	155	160	150	150
Width of brain case at middle of temporal fossae	125	125	120	110	130	115	115	115	125	115	120	125	120	110	115	125	115	120	125	115	120	115	—	—	—	—	115	110	120	110	100
Distance between orbit and base of horn core	130	120	105	120	125	145	115	115	135	135	115	110	125	115	115	130	110	130	110	125	115	130	125	—	120	120	100	115	120	—	110
Height of occiput from basion to lambdoid crest	110	115	115	105	115	110	110	120	120	105	105	115	120	115	105	115	115	120	120	120	115	115	—	—	—	—	105	105	—	—	110
Height from basion to vertex	180	225	210	200	205	190	205	180	240	185	185	210	200	195	185	205	200	190	215	195	210	200	—	—	—	—	160	155	—	—	160
Occiput height index $\left(\frac{\text{basion-lambdoid crest x 100}}{\text{basion-vertex}}\right)$	61	51	55	53	56	58	54	67	50	57	57	55	60	59	57	56	58	63	56	62	55	58	—	—	—	—	66	68	—	—	69
Angle between frontal and occipital planes	75°	70°	70°	75°	75°	75°	75°	75°	65°	70°	70°	75°	75°	70°	75°	70°	70°	70°	65°	80°	70°	75°	—	—	—	—	80°	80°	—	—	80°
Height of skull from palatines to nasal	140	150	140	150	140	140	150	140	140	135	145	145	150	150	140	155	155	150	165	145	145	145	—	—	—	—	140	140	—	—	140
Diverging angle of horn cores	95°	100°	110°	110°	100°	95°	110°	95°	90°	85°	85°	105°	80°	85°	100°	105°	105°	85°	115°	95°	95°	105°	90°	100°	100°	95°	65°	50°	60°	50°	45°
Horn core, horizontal diameter at base	90	110	100	100	100	100	95	95	110	85	90	95	105	90	—	100	95	95	105	95	95	105	110	100	105	90	60	45	50	40	45
Vertical diameter at right angles to longitudinal axis	70	75	—	—	65	70	—	—	—	60	—	—	—	—	—	—	—	—	—	—	—	75	75	70	75	65	45	40	40	30	40
Basal circumference of horn core	250	—	—	—	260	270	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	295	295	265	285	245	165	135	140	110	140
Core length on inner curve	380	—	—	—	360	290	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	335	385	260	300	295	160	105	120	90	110
Idem, outer curve	490	—	—	—	445	400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	440	530	360	365	375	200	120	150	115	150
Straight length from upper base to tip	300	—	—	—	280	190	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	215	275	205	250	220	160	100	110	80	105
Index of curvature $\left(\frac{\text{outer curve x 100}}{\text{straight length}}\right)$	163	—	—	—	159	211	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	205	193	176	146	170	125	120	136	144	143
Index of compression $\left(\frac{\text{vert. diam x 100}}{\text{horizontal diam.}}\right)$	78	68	—	—	65	70	—	—	—	71	—	—	—	—	—	—	—	—	—	—	—	71	68	70	71	72	75	89	80	75	89
Index of proportion $\left(\frac{\text{inner curve x 100}}{\text{circumference}}\right)$	152	—	—	—	138	107	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	114	131	98	105	120	97	78	86	82	79
Index of length $\left(\frac{\text{inner curve x 100}}{\text{width of frontals}}\right)$	211	—	—	—	185	141	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	163	188	127	158	148	100	68	75	60	73

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EXPLANATION OF THE PLATES

Plate I

Duboisia santeng (Dubois), Trinil, Java; figs. 1, 3 and 8, skull, Coll. Dub. no. 2037; fig. 1, left view; fig. 3, top view; fig. 8, occipital view; fig. 2, skull, Coll. Dub. no. 2045, occipital view; fig. 4, right mandibular ramus, Coll. Dub. no. 2068d, external view; fig. 5, right mandibular ramus, Coll. Dub. no. 2053, internal view; fig. 6, frontal, Coll. Dub. no. 2048, top view; fig. 7, frontal, Coll. Dub. no. 2049, top view; fig. 9, frontal, Coll. Dub. no. 2048, left view.

Figs. 1-2, 4-5 and 9, $^3/_8$ natural size; figs. 3, 6-7, $^3/_{10}$ natural size; fig. 8, $^1/_2$ natural size.

Plate II

Epileptobos groeneveldtii (Dubois), skull, holotype, Wadegan, Java, Coll. Dub. no. 2766; fig. 1, top view; fig. 2, anterior and left view; fig. 3, occipital view.

All figures $^1/_7$ natural size.

Plate III

Figs. 1-2, *Capricornis sumatraensis* (Bechstein) subsp., cave in Central Sumatra; fig. 1, M^2 dext., Coll. Dub. no. 755c, crown view; fig. 2, M^3 dext., Coll. Dub. no. 6997d, internal view.

Figs. 3-6, *Epileptobos groeneveldtii* (Dubois); fig. 3, top of skull, Kedoeng Broeboes, Java, Coll. Dub. no. 489a, occipital view; figs. 4 and 6, skull, Kedoeng Nojo, Java, Coll. Dub. no. 2765; fig. 4, occipital view; fig. 6, left view; fig. 5, skull, Kebon Doeren, Java, Coll. Dub. no. 2786, occipital view.

Figs. 1-2, $^{3}/_{5}$ natural size; fig. 3 $\frac{1}{2}$ natural size; figs. 4 and 6, $^{1}/_{5}$ natural size; fig. 5, $^{3}/_{10}$ natural size.

Plate IV

Fig. 1, *Hemibos triquetricornis* Rütimeyer, skull and mandible, Mahrawaia, Punjab, Coll. Dub. no. 3107, right view.

Fig. 2, *Bubalus palaeokerabau* Dubois, skull, holotype, Trinil, Java, Coll. Dub. no. 60, top view.

Fig. 3, *Epileptobos groeneveldtii* (Dubois), skull, Kebon Doeren, Java, Coll. Dub. no. 2786, right view.

Fig. 4, *Hemibos acuticornis* (Falconer et Cautley), skull, Haripoor, Punjab, Coll. Dub. no. 3043, top view.

Figs. 1 and 4, $^{1}/_{4}$ natural size; fig. 2, $1/_{10}$ natural size; fig. 3, $^{3}/_{10}$ natural size; fig. 3, $^{3}/_{10}$ natural size.

Plate V

Figs. 1 and 3, *Bubalus palaeokerabau* Dubois, Trinil, Java; fig. 1, right mandibular ramus, Coll. Dub. no. 540, external view; fig. 3, fragment of ramus with P_2-M_3 dext., Coll. Dub. no. 2598, crown view.

Figs. 2 and 4, *Bibos palaesondaicus* Dubois, Trinil, Java; fig. 2, right mandibular ramus, Coll. Dub. no. 336, external view; fig. 4, fragment of ramus with P_2-M_3 dext., Coll. Dub. no. 345, crown view.

Figs. 5-7, *Bibos javanicus* (d'Alton), recent P_2 sin., Leiden Museum, reg. no. 15398; fig. 5, crown view; fig. 6, external view; fig. 7, internal view.

Figs. 8-10, *Bubalus bubalis* (L.), recent P_2 sin., Leiden Museum, cat. ost. c; fig. 8, crown view; fig. 9, external view; fig. 10, internal view.

Figs. 1-2, $^{1}/_{4}$ natural size; figs. 3-4, $^{3}/_{7}$ natural size; figs. 5-10, $^{5}/_{4}$ natural size.

Plate VI

Figs. 1 and 4, *Bibos palaesondaicus* Dubois; fig. 1, male skull, holotype, Trinil, Java, Coll. Dub. no. 2798, occipital view; fig. 4, male skull, Tegoean, Java, Coll. Dub. no. 2797, occipital view.

Figs. 2-3, *Bibos javanicus* (d'Alton), recent male skulls from Java; fig. 2, Leiden Museum, reg. no. 15384, occipital view; fig. 3, Leiden Museum, reg. no. 15394, occipital view.

Figs. 1 and 3, $^{1}/_{7}$ natural size; fig. 2, $^{1}/_{6}$ natural size; fig. 4, $^{1}/_{5}$ natural size.

Plate VII

Bibos palaesondaicus Dubois; figs. 1 and 4, male skull, Tegoean, Java, Coll. Dub. no. 2801; fig. 1, frontal view; fig. 4, occipital view; figs. 2-3, male skull, Trinil, Java, Coll. Dub. no. 2774; fig. 2, frontal view; fig. 3, occipital view.

Figs. 1 and 4, $^1/_8$ natural size; figs. 2-3, $^1/_7$ natural size.

Plate VIII

Figs. 1 and 4, *Bibos palaesondaicus* Dubois, Trinil, Java; fig. 1, female skull, Coll. Dub. no. 2772, occipital view; fig. 4, female skull, Coll. Dub. no. 2812, occipital view.

Figs. 2-3, *Bibos javanicus* (d'Alton), recent female skulls from Java; fig. 2, Leiden Museum, cat. ost. b, occipital view; fig. 3, Leiden Museum, cat. ost. c, occipital view.

Fig. 1, $^1/_7$ natural size; figs. 2-3, $^1/_4$ natural size; fig. 4, $^3/_{10}$ natural size.

Plate IX

Figs. 1-2, *Bubalus bubalis* (L.); fig. 1, recent P_2 dext., Leiden Museum, reg. no. 4897, crown view; fig. 2, P_2 dext., Sibrambang cave, Sumatra, Coll. Dub. no. 809c, crown view.

Figs. 3-4, *Bibos palaesondaicus* Dubois; fig. 3, male skull, Tegoean, Java, Coll. Dub. no. 2797, frontal view; fig. 4, female skull, Trinil, Java, Coll. Dub. no. 2772, frontal view.

Figs. 5-10, *Bibos javanicus* (d'Alton); figs. 5-6, P_2 dext., Lida Ajer cave, Sumatra, Coll. Dub. no. 742a; fig. 5, internal view; fig. 6, external view; figs. 7-8, recent P_2 dext., Java, Leiden Museum, cat. ost. a; fig. 7, internal view; fig. 8, external view; figs. 9-10, P_2 dext., Lida Ajer cave, Sumatra, Coll. Dub. no. 742b; fig. 9, internal view; fig. 10, external view.

Figs. 1-2, 5-10, $^5/_4$ natural size; figs. 3-4, $^1/_5$ natural size.


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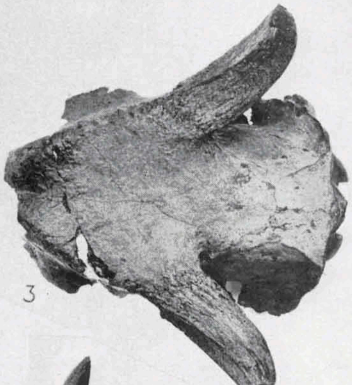
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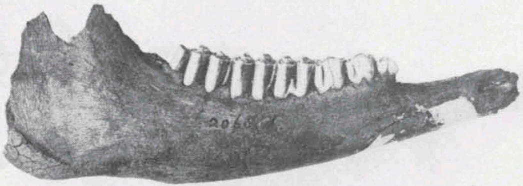
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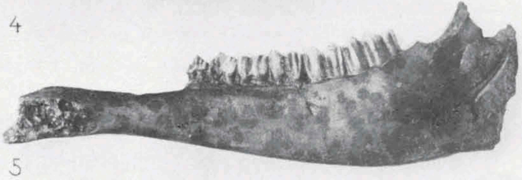
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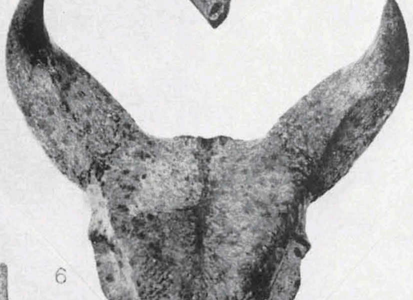
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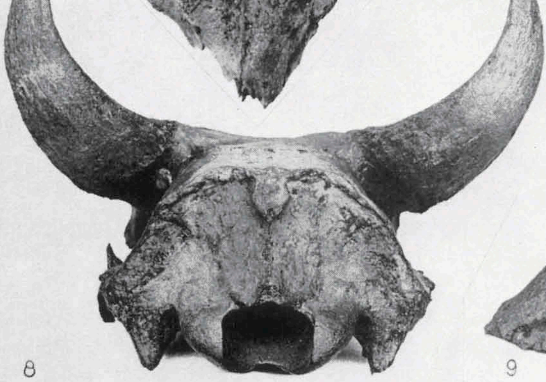
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PLATE II


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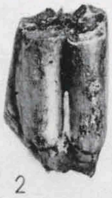
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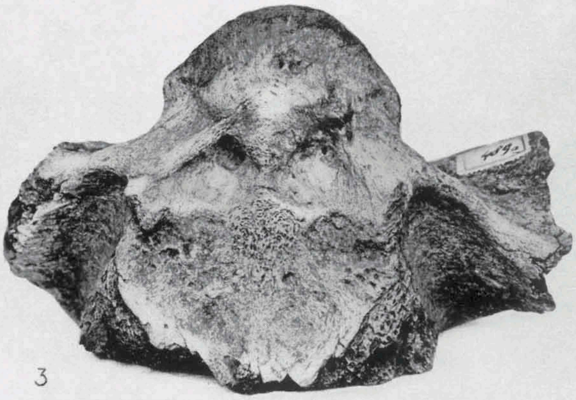
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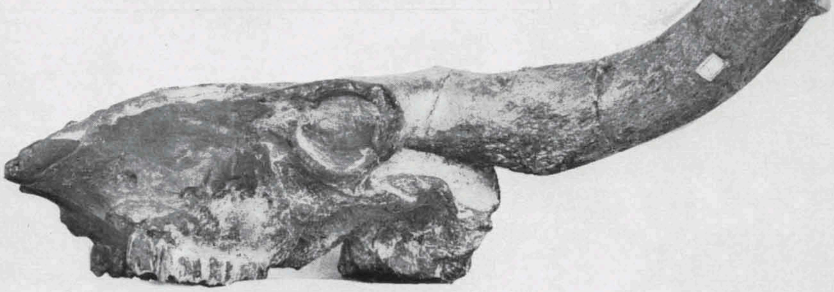
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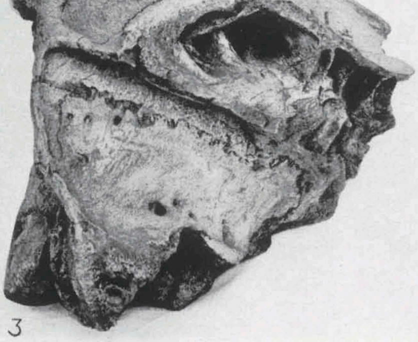
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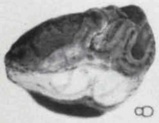
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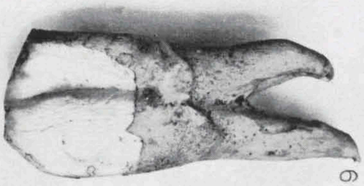
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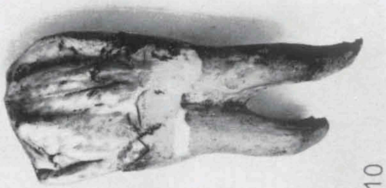
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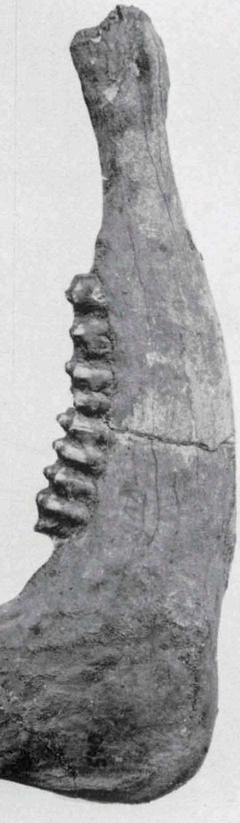
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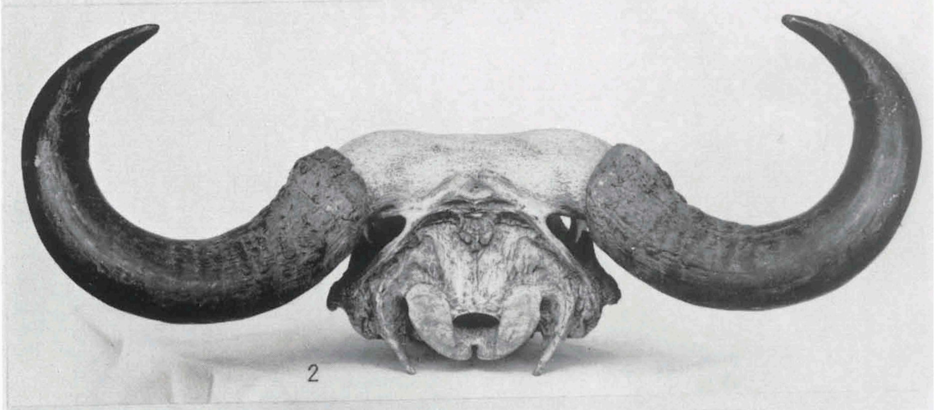

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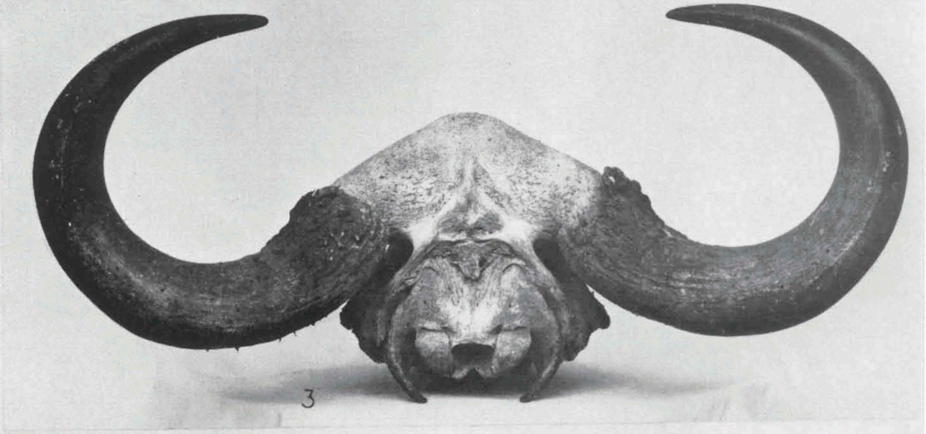

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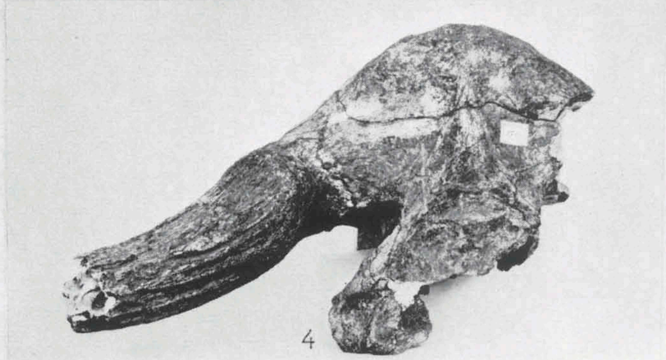

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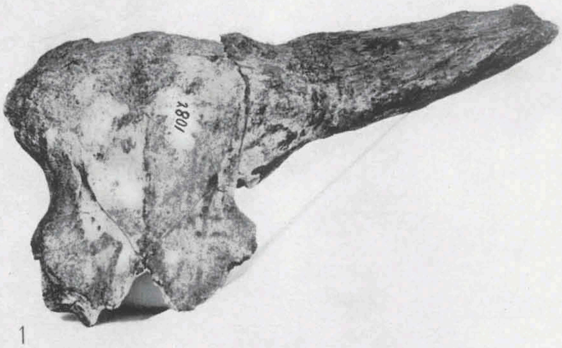

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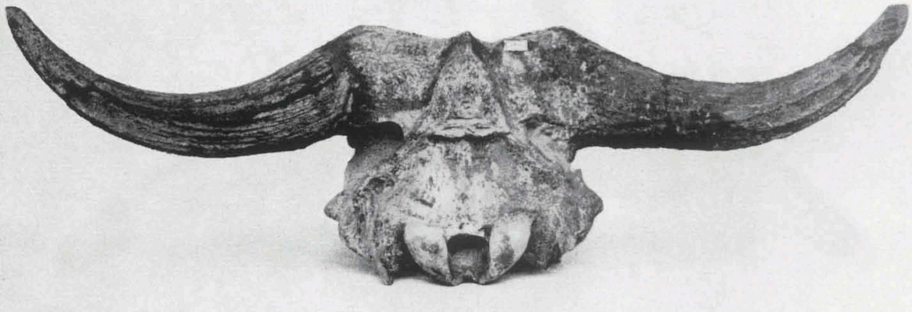

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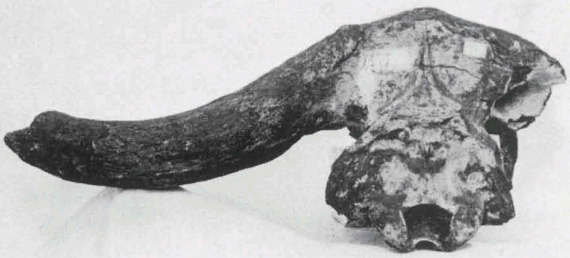

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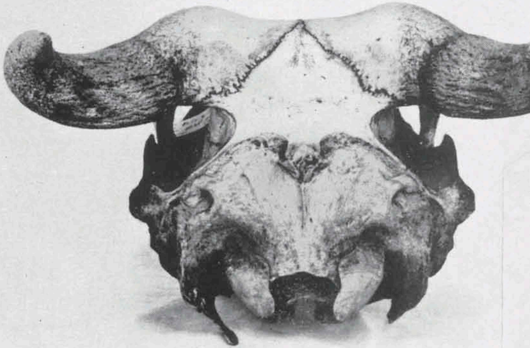

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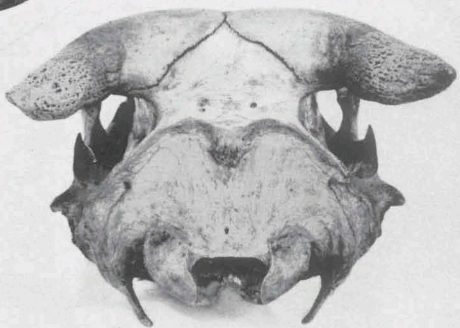

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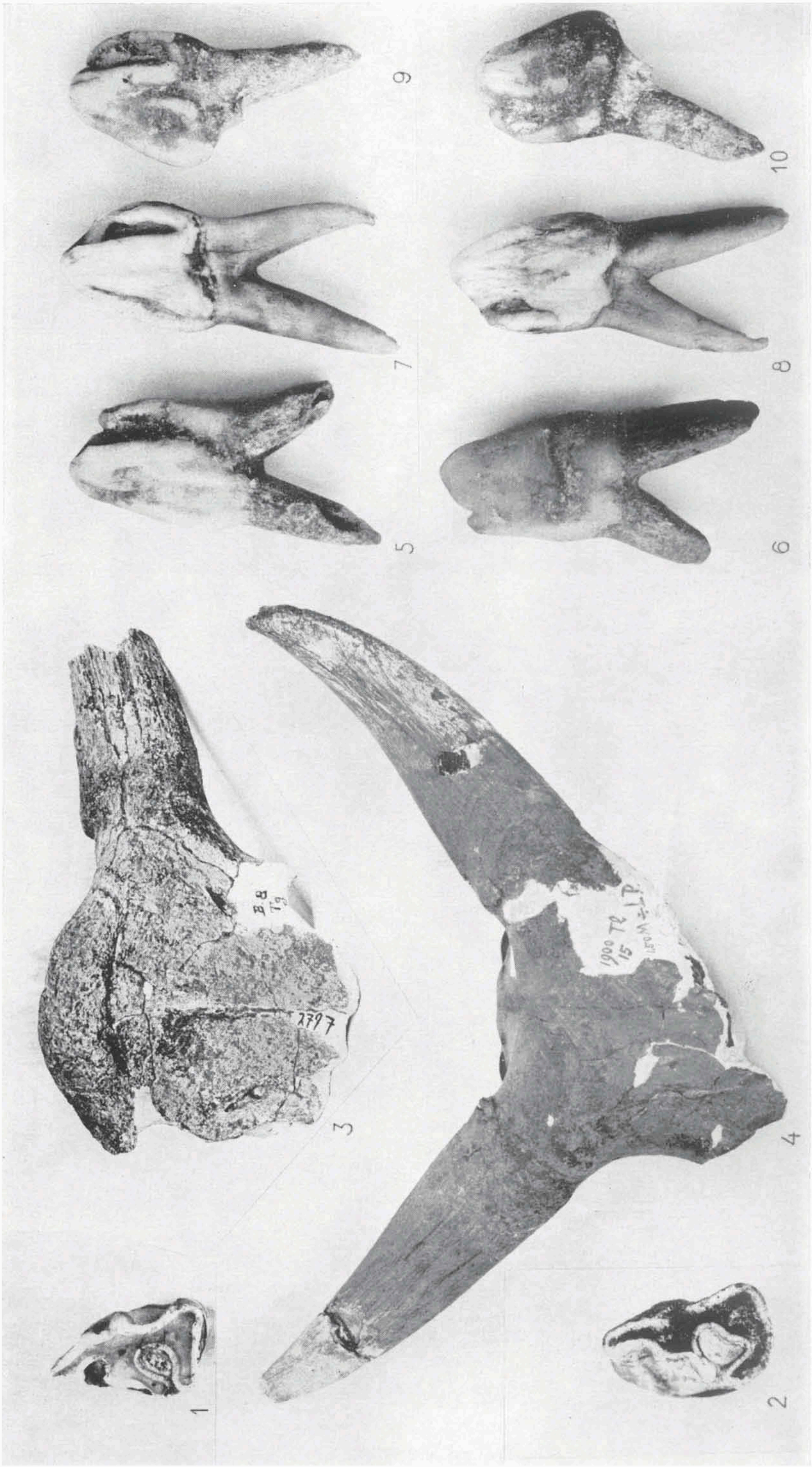
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