Paleontology. — *Pleistocene Vertebrates from Celebes. III. Anoa depressicornis (Smith) subsp., and Babyrousa babyrussa beruensis nov. subsp.* By D. A. HOOIJER. (Communicated by Prof. H. BOSCHMA.)

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The collection of Pleistocene Vertebrates from S. Celebes made by Mr. H. R. VAN HEEKEREN and entrusted to me by Prof. Dr. A. J. BERNET KEMPERS, Head of the Archaeological Survey of the Dutch East Indies, I have already reported upon (HOOIJER, 1948*b*, 1948*c*) contains a small number of teeth referable to two living endemic forms, the anoa and the babirusa. The association of these recent species with forms like *Celebochoerus heekereni* Hooijer, a pigmy archidiskodont elephant, and a gigantic land tortoise (*Testudo margae* Hooijer) which are now extinct, is far from surprising since virtually all living species date back into Pleistocene times. The fossil as well as the prehistoric remains belonging to recent species most often are only larger, in the average, than the recent, and in a number of cases examined it could be proven that the former are subspecifically distinct form the latter. The prehistoric and fossil remains of recent *Dicerorhinus sumatrensis* (Fischer) and *Rhinoceros sondaïcus* Desmarest (HOOIJER, 1946*a*, 1946*b*), *Tapirus indicus* Desmarest (HOOIJER, 1947*b*), *Acanthion brachyurus* (L.) (HOOIJER, 1946*c*), *Panthera tigris* (L.) (HOOIJER, 1947*a*) and *Pongo pygmaeus* (Hoppius) (HOOIJER, 1948*a*) bear evidence of this rule.

Neither the anoa nor the babirusa are living today in the region where their fossil remains were found. In the South-western peninsula of Celebes the anoa still only lives on the Peak of Bonthain in the extreme S. (WEBER, 1890, p. 112; SARASIN, 1905, p. 32), while the babirusa has vanished from the whole of the South-western peninsula of the island (SARASIN, l.c., p. 41). The occurrence of both species in the prehistoric collections from caves near Lamontjong in S. Bone (ca. 60 km E.N.E. of Macassar) and from the neighbourhood of Tjani (Lamontjong), Watampone (Central Bone, ca. 120 km N.E. of Macassar) and Bonthain on the S. coast, described by SARASIN (1905) and DAMMERMAN (1939) respectively, has already established that these forms were more generally distributed over the island in former times than they are now. SARASIN (1905, p. 39/40) reported that the subfossil teeth of the babirusa agree well in size with the recent, but the subfossil teeth of the anoa (l.c., p. 30) average smaller than the recent. From the latter fact SARASIN inferred that the Southern Celebes anoa may have been smaller than the northern form. DAMMERMAN (1939, p. 64) states to have found no noticeable difference in size between the prehistoric and the recent molars of the anoa, however. The Pleistocene fossils are described and discussed below.

Anoa depressicornis (Smith) subsp.

Our Pleistocene material of the anoa consists of four teeth, viz., P_4–M_3 dext. (pl. I, fig. 1). They are embedded in a matrix consisting of calcite grains of irregular form and containing some grains of quartz and alkaline felspar. The specimen originates from Sompoh near Tjabengè (Sopeng district), about 100 km N.E. of Macassar in S. Celebes.

Parts of the external surfaces of the teeth only were exposed when I received the specimen. The external lobes of the teeth have split vertically and the fissures are filled with matrix. Cement has completely weathered off. The crown surfaces of the teeth are incomplete; the V-shaped fossae in the median antero-posterior line of the crowns were found but the higher internal surfaces of the inner cusps are missing. The specimen is much distorted too: M_2 is on a lower level than M_3 while M_1 and P_4 are displaced inward. The posterior portion of M_1 and the anterior portion of M_2 are missing.

Of the P_4 the whole of the outer surface of the crown is preserved. The broad anterior lobe or protoconid exhibits a few vertical cracks, whereas the postero-external pillar or hypoconid has split all over its length. The protoconid is at least 21 mm high from the base to the worn edge, the roots are missing. It is regularly convex antero-posteriorly above and becomes more flattened at the base, especially anteriorly where a very small rudiment of a cingulum is seen. From above downward the protoconid is very slightly concave. Apparently it did not decrease in antero-posterior diameter (about 10 mm) up to the crown edge which is highest in the middle. It is separated from the hypoconid by a narrow vertical groove in which cement has completely gone. At the lower as well as at the upper border of the crown the groove flattens out; it is, therefore, deepest in the middle of its course. The hypoconid forms a straight and narrow vertical ridge, 19 mm in height and about 2.5 mm wide (it measures 3 mm antero-posteriorly but the vertical fissure is about 0.5 mm wide).

A small portion of the P_3 is preserved; it consists of the upper part of the hypoconid ridge, only about 6 mm high, and a very small adjacent portion of the protoconid surface. The groove in front of the hypoconid is decidedly less deep than that in P_4.

Of the M_1 the protoconid is broken and distorted. Its height may have been about 21 mm, the antero-posterior diameter 8 mm. It is regularly convex from before backward with no indication of a median rib. The base of an accessory column in the vertical groove separating it from the hypoconid is preserved. The enamel figure on the crown shows the paraconid to have possessed a strong median rib on its outer surface, but the inner surface of the paraconid is not preserved. Of the hypoconid only part of the anterior surface is seen, the main body of it is missing as well as that of the protoconid of M_2. The M_2 is displaced outward relative to M_1 and P_4 and is much crushed. The posterior surface of the protoconid is broken and in the vertical groove separating it from the hypoconid there is no accessory column. The hypoconid presents a vertical fissure that widens toward the roots which are again missing. Its total height is about 28 mm; antero-posteriorly it measures about 9 mm. The posterior surface is flattened and there is no trace of a median vertical rib on the outer side. From above downward the hypoconid may have been slightly concave.

The M_3 consists of three lobes, the anterior and the middle of which are badly broken; along the vertical fissures that run through them parts of the enamel have broken off especially toward the worn edge. The height of the crown is about 33 mm. The anterior surface of the protoconid as well as the posterior surface of the hypoconid are flattened, and the convexity of these lobes is most marked in the center without, however, forming median ribs. The groove between protoconid and hypoconid is narrow and deep. The fossae on the crown show the inner cusps to have possessed outer median vertical ribs; the internal surface of the molar is lost. The talonid is broken above and below and is shorter antero-posteriorly than the two main lobes. It is separated from the hypoconid by a wide groove. The talonid is well convex antero-posteriorly, narrows toward its summit and possesses a posterior keel, most marked above.

I can find no characters to distinguish the present fossil teeth from those of the living anoa. The lengths of P_4 and M_3 also are within the range of variation of these measurements in four mandibles of the latter species (table 1). In *Bubalus mindorensis* Heude, which is very near in

TABLE 1.

Measurements of fossil and recent molars of *Anoa depressicornis* (Smith) subsp. and of recent *Bubalus mindorensis* Heude.

	Anoa depressicornis (Smith) subsp. Leiden Museum					*Bubalus mindorensis* Heude Leiden Mus.	
	Sompoh	cat. a	cat. b	cat. c	cat. d	cat. a	cat. b
Length of P_4	13.5	14.5	14	12.5	13	15.5	16
Length of M_3	25	27	25	23.5	24	30	30

dimensions to the fossil, all lower molars have well-developed accessory outer columns instead of M_1 exclusively as is the case in our fossil specimen, which is typical of the anoa (HELLER, 1889, p. 17). Accessory outer columns, however, may occasionally develop in M_2 and M_3 of the anoa too (HELLER, l.c.), and in two of the Leiden Museum specimens (cat. a and b) these columns have slightly developed. In *Bubalus mindorensis* the protoconid of the P_4 possesses a median outer rib especially marked off posteriorly; this makes the vertical groove between protoconid and hypoconid $\sqcup$ shaped instead of V shaped as is the case in the anoa in which the protoconid is gradually convex from before backward. The molars of the anoa and our fossil specimen are distinguishable from those of *Bubalus mindorensis* by the same character: the outer lobes are not pinched in anteriorly and posteriorly as are those of *Bubalus*, thereby producing median ribs on protoconid and hypoconid in *Bubalus* that have not developed in *Anoa*. Unfortunately it is impossible to ascertain whether the anterior transverse valley on the internal side of P_4 is blocked or open, as it is in *Anoa* and *Bubalus* respectively (PILGRIM, 1939, p. 255). The distinguishing character I found is not mentioned by PILGRIM, and the presence of median ribs on the outer folds of the lower molars indeed does not seem to be a hard and fast rule in the genus *Bubalus*; in some specimens of *Bubalus bubalis* (L.) and *Bubalus palaeokerabau* Dubois they have hardly developed. Since the fossil teeth are absolutely indistinguishable from those of *Anoa depressicornis* (Smith) they may be classed with that species. I should have expected the fossil teeth to be larger than the recent, as is evident from what has been stated in the introduction of the present paper.

As remarked already above, SARASIN found the subfossil molars of the anoa to average smaller than the recent, while DAMMERMAN found no difference in size between the recent and his subfossil material of the anoa. Neither SARASIN nor DAMMERMAN remark upon the subspecies of *Anoa depressicornis* to which their material for comparison belongs. Besides *A. d. depressicornis* (Smith) typically from the Northern peninsula of Celebes there is also a smaller race, *A. d. fergusoni* (Lydekker), unfortunately without exact type locality, that has been recorded from the high forested mountains of the central region of Toradja and from the high districts of Binuwang on the W. coast of the island, at about lat. 3° 30′ S. and to which probably also the anoas reported from the Peak of Bonthain belong (HARPER, 1945, pp. 550—554). Skull measurements of the smaller race are not known, but if *A. d. fergusoni* is represented in the series of mostly unlocalized skulls of the anoa preserved in various European Museums recorded by HELLER (1889, p. 24) the difference in size is not considerable. HELLER gives the measurements of 25 skulls; the series is arranged from the largest to the smallest but only upon no. XIX they become markedly smaller. Nos. XXII and XXIII are in the Leiden Museum (cat. g and f) and the latter skulls are not adult, M_3 being still unerupted. Nos. XX and XXI, from German Museums, being very near in size to the Leiden Museum skulls, most probably are not yet adult too. The basal length of the 19 remaining and all probably adult skulls varies from 260 to 290 mm only, the zygomatic width from 120 to 141 mm. Skulls a and b in the Leiden Museum, which are nos. I and VII of HELLER's list, originate from Tondano and Menado respectively and they may be taken as representing *A. d. depressicornis*. Their teeth are larger than those of the fossil specimen. Skulls c and d of the Leiden Museum collection (nos. XVIII and IX in HELLER's table) were collected by REINWARDT and are without a record for the exact locality. They have teeth that are smaller than their fossil homologues (table 1). If the latter skulls represent *A. d. fergusoni*, this would link our fossil specimen up with the latter race rather than with the larger *A. d. depressicornis*.

Babyrousa babyrussa beruensis nov. subsp.

Diagnosis: Molars identical in specific characters to those of recent *Babyrousa babyrussa babyrussa* (L.) from Buru and of *B. b. alfurus* (Lesson) from Celebes, but most often distinctly larger (see measurements).

Holotype: An M_3 dext. described and figured in the present paper (pl. I, fig. 2).

Paratypes: Two specimens of M_3 (B and C), an M^2 dext. and an M^3 sin.

Locality: Holotype, and M_3 specimen C, as well as M^3: Beru; M_3 specimen B and M^2: Sompoh, 12 km N. of Beru, near Tjabengè (Sopeng district), about 100 km N.E. of Macassar, S. Celebes.

Age: Pleistocene.

The best preserved specimen is the holotype from Beru. It is an M_3 of the right side, complete, in a fragment of the ramus (pl. I, fig. 2). The plane of wear is oblique, the external cusps (protoconid and hypoconid) are much more worn down than the internal (metaconid and entoconid). These four main cusps are arranged in two transverse pairs, behind which there is a median lobe of the hypoconulid followed by a semicircular posterior portion of the hypoconulid or "talon".

The metaconid is the biggest of the main cusps, and is, like the entoconid behind it, modelled by wear into a chisel-shaped column with the transverse cutting edges falling off toward the outer side. Between these two inner cusps there is a wide valley that opens to the inner surface down to 2.5 mm above the crown base. The transverse valley is blocked in the middle portion of the tooth by ridges connecting the metaconid with the hypoconid, but it is as deep as its inner portion again between the outer cusps, and even wider due to the latter having less well developed than the inner cusps. The groove separating the metaconid from the protoconid has not yet disappeared by wear, but entoconid and hypoconid have just become confluent in the median line. The ridge between metaconid and hypoconid is crossed by a groove indicating the limit between the two cusps. The entoconid narrows distinctly toward the median line of the crown, as shown by grooves marking off this cusp in front and behind. The tooth is slightly wider over the entoconid and the hypoconid than in front but narrows distinctly backward. The semicircular portion of the hypoconulid, or "talon", that is subdivided by an antero-posterior groove into two parts of which the external is the larger, is placed at some distance behind the posterior pair of main cusps, and between them is the central lobe of the hypoconulid, partly wedged in between entoconid and hypoconid. The whole of the crown is surrounded by a feebly developed cingulum, some 2.5 to 3 mm high but hardly visible at some places. In the front surface of the molar there is a hollowed facet caused by interproximal wear with M_2. The dimensions of the present and of the following specimens will be found in table 2 below.

D. A. HOOIJER: *Pleistocene Vertebrates from Celebes. III. Anoa depressicornis (Smith) subsp., and Babyrousa babyrussa beruensis nov. subsp.*

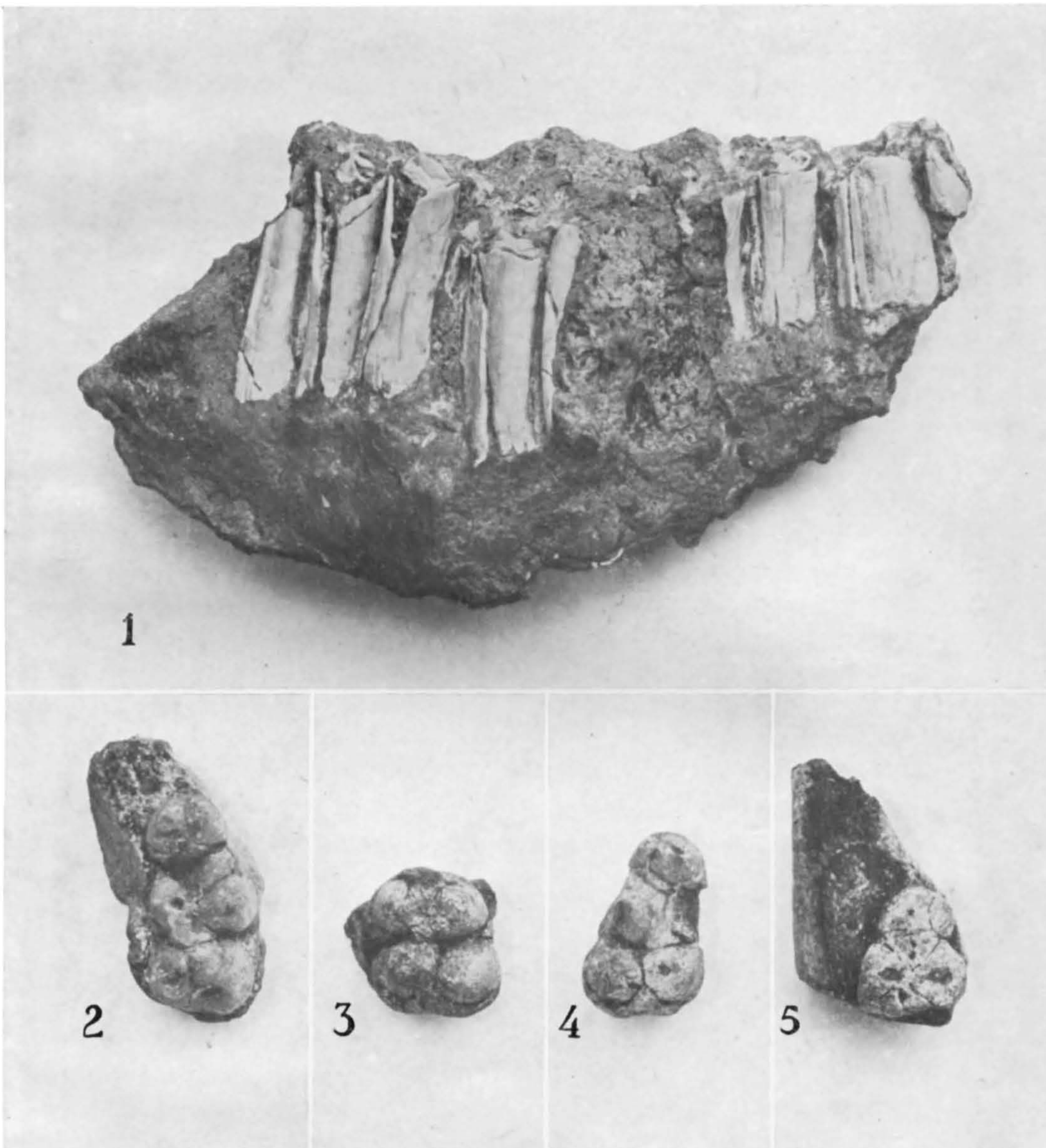

Fig. 1. *Anoa depressicornis* (Smith) subsp.; P_4—M_3 dext., Sompoh, S. Celebes, outer view.

Figs. 2—5. *Babyrousa babyrussa beruensis* nov. subsp.; Fig. 2, M_3 dext. (holotype), Beru, S. Celebes, crown view; Fig. 3, M^2 dext., Sompoh, S. Celebes, crown view; Fig. 4, M^3 sin., Beru, S. Celebes, crown view; Fig. 5, M_3 dext., (specimen C), Beru, S. Celebes, crown view. All figures natural size.

The second tooth to be described (specimen B) is also an M_3 dext., but originating from Sompoh. The protoconid has broken off and the stage of wear is more advanced than that of the holotype, but in all its characters the present specimen is similar to the last with the exception of the shape of the central hypoconulid lobe. The latter has less well developed in the Sompoh molar and consequently the "talon" is shorter. The united antero-posterior diameter of the two internal cusps is the same as that in the holotype, viz., 20 mm, but the length of the whole molar is somewhat shorter. The cingulum is less well marked than that in the holotype.

Our third specimen (C) of lower last molars (pl. I, fig. 5) is again of the right side, and originates from Beru. The anterior pair of cusps has broken off. The limiting grooves of the hypoconid and the entoconid, both narrowing almost to a point in the midline of the tooth, are well seen. The central lobe of the hypoconulid is intermediate in development between those of the foregoing molars; it is defined by grooves as a triangular structure separating the main cusps from the semicircular posterior portion. The latter is crossed by a groove distinctly to the internal side of the median axis of the crown. Dimensions are given in table 2.

From the upper jaw we have two fossil molars, an M^2 dext. and an M^3 sin. The former originates from Sompoh and is entire, though somewhat weathered (pl. I, fig. 3). It has just been touched by wear and has an interproximal wear facet only in front. The cusps are strong and simply built without marked vertical grooving of the enamel. The internal (protocone and metaconule) are higher than the external (paracone and metacone) and the transverse pairs formed by these cusps are slightly oblique: the internal cusps are placed more posteriorly than the external. The anterior cingulum is high in the middle and wide at the base; at the antero-external and antero-internal angles of the crown it terminates hook-shapedly turned up. In the median line its highest point is almost on a level with the saddle between protocone and paracone. The posterior cingulum is narrower but even slightly higher than that at the anterior side. The transverse valley which is blocked in the middle has accessory cusplets both at its internal and at its external entrance, evidently formations of the cingulum that is otherwise lacking at the inner and outer sides of the crown. The dimensions are given in table 2.

The last specimen is an M^3 sin., from Beru (pl. I, fig. 4). It is shorter and wider than the M_3 described above and narrows distinctly from front to back. The greater part of the metaconule is lost. Of the two anterior cusps the protocone is the larger; both are rounded and not grooved. The metacone is placed more inward than the paracone and is apparently the smallest cusp; it is separated from the paracone in front by a deep valley. A central antero-posteriorly elongated lobe separates the metacone from the metaconule and also partly fills the valley between metaconule and protocone. The central lobe turns outward behind the metacone and forms a distinct accessory cusplet above the external cingulum between the metacone and the talon. The latter is small but has an accessory outer tubercle. The cingulum forms a distinct ledge around the crown and rises in front into a high central point like that in the M^2.

TABLE 2.
Measurements of fossil and recent molars of *Babyrousa babyrussa* (L.)

	B.b. beruensis nov. subsp.			*B.b. babyrussa* (L.) (Buru)	*B.b. alfurus* (Lesson) (Celebes)
	holo-type	B	C		
M_3					
Length	30.5	28.2	—	22.7—26.7	24.5—27.4 (29.6)
Ant. width	14.6	—	—	12.9—14.1	12.9—14.7 (15.8)
Post. width	15.3	14.6	14.3	11.7—14.2	12.0—14.6 (14.9)
M^2					
Length		20.2		15.1—17.6	16.8—19.4 (20.0)
Ant. width		18.0		13.8—15.5	15.0—16.2 (17.5)
Post. width		17.6		12.4—15.9	13.6—16.6 (17.2)
M^3					
Length		25.4		20.4—23.4	22.7—25.7
Ant. width		17.1		14.5—16.7	15.0—16.7 (17.7)

The present fossil molars correspond so exactly with the homologous teeth of the babirusa that there can be no doubt in referring them to the same species. There is, however, a difference in size. As is evident from the inspection of table 2 the dimensions of the fossil molars are invariably greater than those found in the Buru babirusa (a series of 13 skulls in the Leiden Museum), that is slightly smaller than the recent Celebean form. The variation limits of the tooth dimensions in a series of 9 skulls of the babirusa from Celebes is given in the last column of table 2, and in parentheses I added the maximum figures found in a series of 19 babirusa skulls which have no record for the exact locality. The holotype M_3 is longer and has a greater width over entoconid and hypoconid than all recent specimens of M_3, and in its anterior width it is exceeded only by 5 out of the 40 recent homologues. The Sompoh M_3 (specimen B) is longer than all but one and wider than all but another out of the latter, while the smallest of the fossil specimens of M_3 (C) is still wider than 38 out of the 40 recent specimens. The M^2 is larger in all dimensions than its homologue in all of the 41 recent skulls. The M^3 is longer than all but 2 of the recent M^3, and is exceeded in width likewise only by 2 (other than those that are longer) out of the 40 recent specimens of M^3.

Thus four out of the five molars of the Pleistocene Celebean form of babirusa are larger than their homologues in a series of 40 recent skulls and the fifth molar (a fragment) still stands third for the greatest width in this long series. I have no babirusa material from the Sula Islands, but this form, *Babyrousa babyrussa frosti* (Thomas, 1920, p. 187) is stated to be slightly smaller even than the Buru race. Consequently it is rendered certain that the Pleistocene Celebean babirusa averages larger than the largest of the recent races of the species, viz., *B. b. alfurus* (Lesson) (= *B. b. celebensis* (Deninger, 1909, p. 185)), and therefore it may be described as a separate subspecies. *Babyrousa babyrussa beruensis* nov. subsp. bears evidence of the diminution in size which the babirusa has undergone in the island of Celebes since Pleistocene times, perfectly in accordance with the rule formulated on p. 1322. As has been stated above it is not yet certain whether the anoa presents an exception to this rule. In the island of Buru the decrease in dimensions has proceeded further, the Buru babirusa being smaller, in the average, than the Celebean race. Similar differences in size are well known to exist between insular races of one and the same species.

A number of mammalian species occurring with the Pleistocene, prehistoric and recent faunae in the islands of Java and Sumatra as well as on the Asiatic continent have now been studied intensively enough to enable us to state that the recent subspecies evolved in situ from racially distinct populations that existed already in the Pleistocene (HOOIJER, 1946b, 1946c, p. 265; 1947a, p. 12—13; 1947b, p. 288; 1948a, pp. 279, 292). For Celebes and the Eastern part of the Malay Archipelago we are merely at the beginning of this work. But as a result of the lucky finds of Mr. VAN HEEKEREN at Beru and at Sompoh in S. Celebes we know now already more of the Pleistocene fauna of this island than of that of the large continental islands of Sumatra and Borneo! The latter islands, because of their position on the Sunda shelf certainly yield much of the fossil species of Vertebrates found in Java. Celebes appears to have as faunistically distinct from the other Greater Sunda Islands in the Pleistocene as it is at the present day; two of its endemic forms have already come to light, and others will doubtless turn up in the collections to be made. The fossil teeth and bones found by Mr. VAN HEEKEREN consist of isolated specimens washed out of their deposits. The determination of the exact geologic age of the fossils when found in situ will be a matter of great evolutionary interest.

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