A REVIEW OF FOSSIL AND PREHISTORIC REMAINS OF RHINOCEROSES OF BORNEO

Earl of Cranbrook

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A. Dental material

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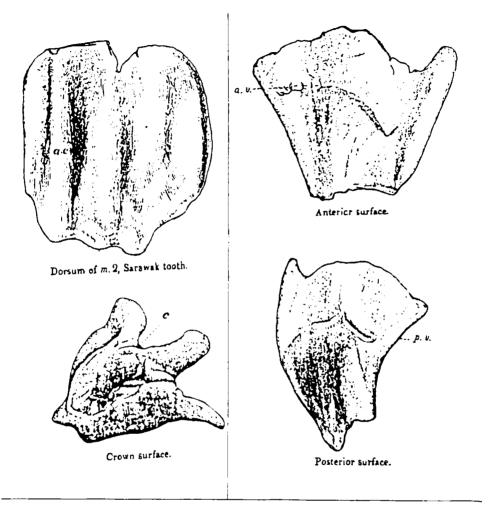
Introduction

Two rhinoceros species occur on continental Southeast Asia, the Javan or Lesser one-horned rhinoceros, *Rhinoceros sondaicus*, and the Sumatran or Asian two-horned rhinoceros, *Dicerorhinus sumatrensis*. In island Southeast Asia, it is known that both species are (or were, in historic times) present on Sumatra, but only the former on Java.

Rhinoceroses also occur on Borneo. but their identity has been a matter of uncertainty and controversy. The first record in scientific literature was that of S. Müller (1840). He reported the evidence of a local informant ('Bejadjoe-Dajakker') who sketched a large, one-horned rhinoceros, the precise identification of which had to remain conjectural.

The Royal Belgian Institute of Natural Sciences contains a mounted skeleton of *R. sondaicus*, reg. no. 1207, catalogued with the provenance "Borneo". collector "Henrici". Recent research has confirmed that H.A. Henrici served under the Dutch administration in southeastern Borneo from 1833 for several years, and that he collected specimens (including rhinoceros skeletons) which were purchased in 1839 by the Belgian authorities. The documentation of specimen no. 1207, however, is not yet fully clarified and the authenticity of its provenance not firmly established. A full report on the Henrici collection of mammals is in preparation.

The presence of *R. sondaicus* was apparently supported by a skull purchased by the British Museum in 1859, as part of a small collection of mammal specimens purportedly from Borneo. This skull (reg. no. BM 59.8.16.1) was described as *Rhinoceros nasalis* by Gray (1867) and subsequently catalogued under this name (Gray, 1869), but its distinctness from '*Rhinoceros javanicus*' (i. e. *sondaicus*) was poorly established. Neither the species R. nasalis, nor its location were generally accepted by contemporary zoologists (e. g. Murray, 1868)¹ Almost immediately, however, further confirmation of the existence of R. *sondaicus* was apparently provided by two subfossil molars from Sarawak, sent to London by Rajah James Brooke and identified by Busk (1869) after a painstaking comparison of the dental morphology of the two species.





Busk's illustration of the rhinoceros molar from Sarawak. Reproduced from the *Proceedings* of the Zoological Society of London, 1869.

Yet during the 1860s and subsequently, other specimens of rhinoceros from Borneo that began to accumulate in the museums of Europe, and indeed also in Kuching and Buitenzorg, proved without exception to be the smaller, two-horned *Dicerorhinus sumatrensis* (see Rookmaaker, 1977, for a historical review). Based on local experience of more than 20 years, A. H. Everett (1893) concluded that there was no reliable evidence to confirm the existence of R. sondaicus among the fauna of Borneo, while D. sumatrensis was undoubtedly present. Charles Hose (1893), equally experienced, listed only D. sumatrensis.

In the early decades of the 20th century, some reviewers compromised by including Borneo in the range of both species (e.g., Raven, 1935). Others accepted the opinion favoured by local authors (e. g., Banks, 1931) that only D. sumatrensis occurred. The latter view was strengthened by Hooijer's (1946a) reassessment of the dental characters relied on by Busk (1869), establishing not only that they were inconclusive in separating the species but also that the two subfossil molars in question possessed one discernible character positively indicating D. sumatrensis. Groves (1967) confirmed that R. nasalis Gray was indeed indistinguishable from R. s. sondaicus of Java, and assumed that its origin was on that island. Certainly, the provenance of this specimen had been accepted with reservation at the time. For instance. Busk (1869) wrote: 'As this testimony rests, so far as I am aware, solely upon the statement of a dealer, it may not be regarded as of much weight'. Its attribution to Borneo is undoubtedly weakened by the uncertain provenance of the other specimens with which it is associated. Two of these, the babirusa and the warted pig, do not occur in Borneo. and one other, the tiger, is a doubtful member of the recent fauna (Medway, 1977a). Rookmaaker (1977) fairly reflected the consensus of contemporary opinion when he wrote "with absolute certainly that sondaicus never existed [in Borneo]".

Yet this statement of itself creates a puzzle. Why, when lowered Pleistocene sea levels (Verstappen, 1975) evidently facilitated faunal exchange between the mainland and large islands of the Sunda shelf. should one species of rhinoceros have succeeded in reaching Borneo and not the other?

Palaeontological work has shown that the tapir, *Tapirus indicus*, was formerly present on Java (Hooijer, 1947), and also on Borneo where it survived to at least 6000 B. C. (Medway, 1961). Like the Javan rhinoceros, the tapir was the subject of unconfirmed reports by early European visitors to Borneo (see Medway, 1977a: 143). The evidence presented below now demonstrates that the Javan rhinoceros was also a member of the late Quaternary fauna of Borneo. May not it, too, have survived long enough to have been seen in the upper Kahayan by Müller's

Beyaju informant, been collected by H.A. Henrici, and even taken for the dealer who supplied the British Museum with the type specimen of R, nasalis?

Archaeological material

1. Busk's teeth, from I Division, Sarawak

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As already mentioned, the first fossil remains of rhinoceros found in Borneo were two unerupted upper second molars (right and left), sent to Sir Charles Lyell by Rajah James Brooke and later examined by George Busk. In a covering letter, the Rajah admitted that he had forgotten the exact locality in which the teeth were found, but he was able to say positively that they were picked up in the 'Sarawak country', i. e. the present I Division. From their brittle nature, colour, smell when wetted and the material found in hollows in the teeth, Busk (1869) deduced that the specimens had lain for a long time in peaty soil containing much iron and vegetable matter, and not in a cave.

The specimens were deposited in the Hunterian Museum, Royal College of Surgeons, London, reg. no. 2140 (Flower & Garson, 1884: 420). They were, unfortunately, destroyed when this museum was bombed in 1941 (E. Allen, *in litt.* 1982). The original illustrations are reproduced as Figure 1.

2. Everett's collections

The next collections, in chronological order, were those obtained by A. H. Everett from caves in Sarawak, evidently in the gold mining district of Bau (approx. $110^{\circ} 10^{\circ}$ E, $1^{\circ} 25^{\circ}$ N) during 1878 - 79 (Evans *et al.*, 1879). The material is now preserved in the British Museum (Natural History). Reference has already been made to remains of dogs (Medway, 1977b) and pigs (Cranbrook, 1979) from this collection.

Everett himself did not report the presence of rhinoceros remains among his finds (Everett, Evans & Busk, 1880). His collections were, however shipped to London where they evidently received the attention of experts. A first selection from the material was deposited by P. L. Sclater in the British Museum, including both dental and post-cranial elements of rhinoceros. These were catalogued by Lydekker (1886: 129) who identified them provisionally as *Rhinoceros sondaicus*, as follows: M. 1968. Two first or second upper true molars of opposite sides and three lower cheek teeth, provisonally referred to this species...

M. 1969 – 70. Several bones (comprising part of a scapula. radius, the complete third metatarsal, a broken lateral metapodial and two fragments of a cervical vertebra) associated with the preceeding specimens.

These two upper molars were not available for examination by Hooijer (1946a), but were later photographed for Medway (1965: plate XXI) who discussed the features displayed and concluded that the teeth were identifiable as D. sumatrensis rather than R. sondaicus.

Some years after the first presentation, further examples of Everett's Sarawak collections were received by the British Museum. The rhinoceros remains were registered as a single lot, as follows:

M. 4154. *Rhinoceros sondaicus*. Three teeth and various bones from auriferous drift in fissures in limestone. Sarawak, Borneo. Presented by A. Everett, Esq., June 1890.

(22)

This material was acquired after the publication of Lydekker's catalogue, and has consequently been largely overlooked. I can find no previously published account of specimens, which are itemised in full below. An inventory is given as Appendix I.

3. Niah caves: Sarawak Museum collections

The first systematic post-war cave excavations by staff of the Sarawak Museum under Tom Harrisson were made at Bau in 1950. The one published report. on work at Gua Bungoh, mentioned bones but offered no identifications; a promised "later report" on bone remains (Harrisson & Tweedie, 1951: 179) never appeared.

The important excavations at Niah (113° 48'E, 3° 45'N) were more productive (T. Harrisson, 1957, 1958). The most striking find among rhinoceros remains was a partly crushed radius that had apparently served as a head-rest ("pillow") in a flexed human burial in the West mouth (T. Harrisson, 1957). In Barbara Harrisson's (1967) classification, this is burial no. 27, classed as "mesolithic", and dated in the range c18.000 – 2.000 B. C. It was. unfortunately, not selected for radiocarbon dating and

palaeoserological study by Brooks *et al.* (1979). In the series of 34 burials of all kinds studied by these authors, the oldest flexed burials were dated within the limits 5675 - 9000 B. C., and none was older than 11.030 B. C. These dates may indicate the likely age of no. 27^2 .

Other remains of rhinoceros from Niah consisted of separate small bones of the feet, six from the levels 0-24 inches to 60-66 inches in the West mouth and one from 18-24 inches in the Lobang Angus mouth, and one tooth from Lobang Angus and fragments of teeth from 12-24 inches down to 60-72 inches in the West mouth (Medway, 1965). Computed C¹⁴ ages of samples taken in the frequentation zone indicated a date of 30,673 \pm 700 B.C. at 72 inches in the West mouth (see combined tabulation in Medway, 1979: Table 1). The agc/depth relationship in Lobang Angus is not known. Tom Harrisson (1966) published only the briefest of preliminary observations on this cave, although the animal remains were reported in some detail by Medway (1967).

Also discovered at Niah was the proximal part of a right fourth metacarpal, heavily mineralised, at $E/W \ 8, \ 6 - 12$ inches, in the West mouth. Its mineralised condition sets this specimen apart from the other mammal bones found in its vicinity at Niah. It was presumably a 'value object', of extraneous origin, transported by man (see Medway, 1965), and its stratigraphic position cannot be taken as an indication of its real age.

4. Lubang Tingalan (=Tinggalan), Baturong caves, Sabah.

Excavations in this cave were carried out under the supervision of Barbara Harrisson in 1966 and 1968. A rhinoceros tooth was recovered from trench TTO/1 in the basal level at 60-78 inches, apparently among a concentration of shells of edible freshwater snails (T. & B. Harrisson, 1971: 101-103).

The tooth was identified as an upper left third deciduous premolar (but in two citations as a premolar) of D. sumatrensis harrissoni, and is illustrated (T. & B. Harrisson, 1971, pl. 21). The present whereabouts of the specimen is not known.

5. Madai caves, Sabah.

The Harrissons also reported the find of a fragmented "rhino molar" (with no other details) from a level of 42-48 inches in a trial trench dug in 1968 in the Agop Atas mouth of Madai caves. Sabah (T. & B. Harrisson, 1971: 90). Once again the specimen cannot now be found, and unfortunately no measurements or other information exist to provide an identification.

Excavation was resumed at Madai caves in 1980 by Sabah Museum staff, with the assistance of Dr. Peter Bellwood of the Australian National University. In late 1980 and again in early 1982, I examined the animal remains from this series of digs, by then in store at the Sabah Museum premises in Kota Kinabalu. A general report on this material is held on file at the Sabah Museum (Cranbrook. unpubl.). A full account of the excavation will be published elsewhere (P. Bellwood, full account to be published by the Sabah Museum 1987).

Rhinoceros remains found among the mammalian bone from the cave known as Agop Sarapad are attributed (below) to *Rhinoceros sondaicus* and *D. sumatrensis*.

Comparative material

The following skeletons have been used to provide measurements of homologues of the archaeological material. They are referred to in tables, etc., in the paragraphs that follow by their museum registration numbers. The localities given are those recorded on specimen labels or in registration documents.

a. In the British Museum (Natural History), South Kensington:

Dicerorhinus sumatrensis

1872.12.31.1	f.	Malay Peninsula
1879.6.14.2	m.	Malacca
1894.9.24.1	m.	Siboga, S.W. Sumatra
1931.5.28.1	m.	Mogok, Burma
1948.12.20.1)		(Rothschild coll.: no sex or
1949.1.11.1)		location)
76.711		(Mounted foot)

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Rhinoceros sondaicus

1861.3.11.1 (=723d)		Java	
1871.12.29.7 (=723f)	m	Sumatra	
1921.5.15.1	f	(subadult)	Tenasserim, 10°N

The sole skeleton of recent D. sumatrensis from Borneo to which h reference has been possible is in the collections of the Zoological Museum, University of Cambridge:

f H6381 Baram district, Borneo.

This specimen, which was collected by Dr. Charles Hose, is of an immature animal. In the upper jaw, the permanent incisors are about to erupt; in the lower, the deciduous incisors are still in use. In both jaws the first permanent molars have recently erupted, being still scarcely worn. In the postcranial skeleton, some of the epiphyses of the long bones of the limbs are fused, others are still discernible, if not detachable. But all foot bones, including the metapodials, have evidently completed growth and no epiphyseal sutures are detectable. As will be seen below, the most significant comparisons are those based on metapodials.

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Two skulls of Dicerorhinus sumatrensis in the Sarawak Museum, c. Kuching, Malaysia, also provided dental measurements. Both are immature, with second upper molars in the process of erupting.

CATALOGUE

Javan rhinoceros, Rhinoceros sondaicus Desmarest

Α. Dental material

1. Left upper fourth deciduous molar; crown only: Agop Sarapad, Madai caves. near Kunak, Sabah; trench L3, between 15 and 20 cm below present cave soil surface. Excavated by Sabah Museum, 1980 (see Bellwood, in prep.). The original tooth is preserved in the Sabah Museum (reg. MAD2, L3, 15-20); an excellent cast has been made for the British Museum (Nat. Hist.) (reg. no. M43073). See Plate 1.

The crown of this shows minimal wear and is in perfect, undamaged condition, a light golden brown in colour, paling to near white along the occlusal margins of the ridges and prominences. In life, it must have been just showing through the gum. Dimensions are given in Table 1, compared with recent specimens and fossil teeth from caves in Sumatra measured by Hooijer (1946a). It should be noted that the crown height is measured as the height of the labial surface of the tooth from the crown base to the occlusal margin. Since the tooth is markedly tapered in profile, this value exceeds the actual height of the highest point of the tooth above the plane of the crown base (=32mm). In addition, because both margins of the labial face are strongly convex, the antero-posterior length at crown base (see Table 1) is exceeded by the greatest antero-posterior length (=48.7mm). The corresponding measurements of H6381 and the Sarawak Museum examples (Table 1) may be compared, although the difficulty in measuring this dimension of a tooth in situ in the skull makes it impossible to assess the precise point in the profile at which the length has been measured.

From Table 1, it is seen that the Madai tooth is intermediate in size between the homologues in recent R. sondaicus and the fossil specimens from Sumatran caves measured by Hooijer (1946a). It is no longer, but distinctly broader than its homologues in recent D. sumatrensis; and only slightly broader than fossils of this species from Sumatra. The relative breadths of anterior and posterior lophs do not serve to separate these samples. Hooijer (1946a:12) has already noted that this character is of little diagnostic value where this particular tooth is concerned.

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TABLE 1

Comparative measurements of fossil and recent upper fourth deciduous molars of *R. sondaicus* and *D. sumatrensis*, in mm. Following Hooijer (1946a) all lengths are measured at the crown base, and the 'transverse ratio' = posterior : anterior dimensions.

Species	Ref./reg. no.	Crown height	Wear	Antero-post. length	Anterior transverse	Posterior transverse	Transverse ratio
R. sondaicus	Madai	39.8	nil	41.5	49.5	46.1	0.93
	B.M. 1865.8.22.1	-	heavy		45.0	38.2	0.85
	Hooijer (1946a) recent	-	-	34-39	41-46	38-42	.8995(2)
-	Hooijer (1946a) fossil	-	-	43,44	50,51	50,47	100,92 (2)
D. sumatrensis	H6381	-	heavy	(43.5) ⁽¹⁾	44.5	37.5	.84
	Hooijer (1946a) recent		-	29-36	38-44	34-41	.8995 ⁽²⁾
	Hooijer (1946a) fossil	-	-	36-45	42-49	38-45	.8493(2)
	Sarawak Museum (1)	22	marked	41.2	43.0	38.9	.90
	Sarawak Museum (2)	12	v. heavy	35.0	(37.8)	$(34.6)^{(3)}$.92

Footnote (1) Measured at the occlusal surface, the crown base being concealed by bone.

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(2) These ratios are derived from individual measurements tabulated by Hooijer (1946a).

(3) The enamel has been lost from the inner part of the crown of this tooth, and it has been necessary to take account of this loss in giving a value to breadth measurements.

Final identification therefore depends on morphological features (see Plate 1). In the following, the tooth conforms with all distinctive characters of R. sondaicus, in contrast to D. sumatrensis, as observed by Hooijer (1946a):

- (a) the anterior cingulum is well developed;
- (b) there is no protocone fold;
- (c) the postsinus is distinctly shallower than the medisinus;
- (d) there is no vertical depression in the anterior surface of the metaloph;
- (e) the crochet springs off from the upper margin of the metaloph.

All D^4 of *D. sumatrensis* that I have been able to examine are well worn. It can still be seen that the example in the jaw of H6381 possesses a pronounced protocone fold, and lacks the anterior cingulum. Those in the Sarawak Museum conform. The total match of the fossil tooth with *R. sondaicus* in each of those five diagnostic characters therefore provides the grounds for a secure identification. As noted above (Introduction), the status of the species in Borneo has been the subject of controversy. This archaeological specimen gives the first positive indication of the former presence of this rhinoceros in Borneo. A sample of freshwater shell from trench L3, from the same approximate depth as this tooth (and the metacarpal of *D. sumatrensis*, No. MAD 2, L3, 10-15, below), has been radiocarbon dated to 9350± 110 B. P., i. e. 7368 B. C. (P. Bellwood, 1983).

B. Postcranial skeleton

2. Part of the proximal articulation of right ulna, comprising of three fragments of bone, recovered separately by the excavators and evidently broken in antiquity. Provenance is as follows:

(a) Agop Sarapad, trench H1, layer 2 between 10-15cm from top of layer;

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 (b) & (c) Agop Sarapad, trench H1, layer 2 at 15 cm from top of layer. Sabah Museum reg. MAD 2, H1, 10-15. See Plate 2(a).

Although not associated at the time of excavation, pieces (a) and (b) fit exactly. The reassembled piece is recognisable as a fragment of the proximal articulation of ulna, showing the following surface features:

- (1) the entire processus anconeus, slightly flaked(after excavation) on one side;
- (2) the entire lateral articular facet, i. e., the semilunar notch; and
- (3) the major part of the interosseous surface, including a well-marked groove terminating at its proximal end in a small nutrient foramen.

The remaining piece (c), cannot be fitted to (a) and (b); it shows the original surface of the bone only on one side. This surface is very rough, drawn out into a series of small papillate surface prominences, such as occur at the insertion of a large tendon. In general outline it matches the lateral surface of the head of the olecranon. The extent of surface sculpturing suggests that the individual was aged.

The reassembled piece, (a) and (b), offers the following measurements:

- (1) The height of processus anconeus, measured at the lateral surface, from the line approximately tangential to the lower margin of the flangelike lateral extension of the upper part of the articular surface, to the upper margin of the process;
- (2) The breadth of processus anconeus in the mediolateral plane;
- (3) A chord across the semilunar notch (=external trochlear facet) from the tip of the processus anconeus to the distal margin of the facet;
- (4) The breadth of the laterally flattened part of the shaft behind the processus anconeus.

These measurements are given in Table 2. It is seen that, while there is overlap between the extant species in two of the measurable characters, there is no overlap in the others. In all measurements, the archaeological specimen (as already noted) is larger than any example of D. sumatrensis available to me but falls in or very near to the range of R. sondaicus. In unquantifiable terms, the sculpturing of the interosseous groove – especially its depth and distinctive border – more closely resembles the examples of R. sondaicus. On the other hand, in neither species are the ulnae of different individuals consistently alike in this character. The variation is such that firm specific distinctions cannot be recognised.

TABLE 2

Reg. no.		М	easuremen	ts
	1	2	3	4
ab, MAD 2 (H1)	46.5	42	71.3	22.5
ondaicus				
1871.12.29.7	47	45	72.6	21.6
1861.3.11.1	42.5	48.4	73.5	19.5
1921.5.15.1	53	43	69.8	23.2
matrensis				
H6381	34.5	33	50.5	14.4
1879.6.14.2	39.1	31.7	51.3	20.4
1894.9.24.1	39.5	31	54.8	21.8
1931.5.28.1	44.6	34.5	60.5	20.0
1948.12.20.1	40.5	30.5	56.5	19.4
1949.1.11.1	39	35.2	56.5	19.8

Measurements of the ulna of rhinoceros in mm⁽¹⁾

(1) For explanation of measurements, see text.

Although (as will become apparent below) the prehistoric populations of *D. sumatrensis* in Borneo were evidently larger than the living form, I feel justified on balance in attributing these ulna fragments to *Rhinoceros sondaicus*.

These specimens were recovered from the base of an ancient shell midden, in Agop Sarapad. The midden was about 15 cm thick, and consisted chiefly of the shells of riverine molluscs, with a small percentage of marine species. Two radiocarbon dates for freshwater shells from this midden, obtained by the laboratory at the Australian National University, denote ages of 9830 & 9010 years, i.e.c.7500 B.C.(P.Bellwood, pers.comm.). It appears that trench L3 (the find spot for the tooth, No. 1. above) contained material washed out from this shell midden and clearly contemporaneous with it. The totality of stratigraphic and dating evidence suggest to the excavator that human frequentation of Agop Sarapad lasted for perhaps a few centuries around the Pleistocene-Holocene boundary (P. Bellwood, pers. comm.).

3. Left ectocuneiform. West mouth, Niah cave, trench Y/3, 54-60 inches depth. Sarawak Museum; unregistered. A fragment only, identified by D. A. Hooijer (see Medway, 1965, Table 1, item 13). At that time, it seemed premature to recognise the presence of R. sondaicus on this evidence alone. The specimen can now be taken as further demonstration of the existence of the larger species in Borneo in the terminal Upper Pleistocene. The only measurement possible is the proximo-distal height between the two chief articular surfaces; at its least, this is 23.5 mm and at its greatest 27mm.

4. A fragmentary lateral proximal phalanx, consisting only of the distal articulating face and a short portion of the shaft. West mouth, Niah cave, trench E/C = C, 48-60 inches. Sarawak Museum; unregistered.

The measurements of this specimen (breadth of articular face 35 mm, greatest anteroposterior width 30 mm) are compatible with *R. sondaicus*, although previously I refrained from making a confident identification (Medway, 1965, Table 1, item 11).

A. Dental material

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1. a & b. Left upper second molar and right upper second molar, unerupted and partially formed. Formerly in the collection of the Hunterian Museum, Royal College of Surgeons, reg. no. 2140; destroyed in 1941. See Figure 1.

The history of these specimens has been outlined above. Busk (1869) published no measurements and none can now be taken. The identification is based on Hooijer's (1946a: 9-11) recognition of the protocone fold, diagnostic of D. *sumatrensis*.

2. Left upper third deciduous molar. Trench TTO/1, at basal level. 60-78 inches, Lubang Tinggalan, Baturong caves, Sabah. Present whereabouts unknown.

The record is based on the identification of Dr. Don Savage (as *D. sumatrensis harrissoni*), reported by T. & B. Harrisson (1971: 101-103; Plate 21).

From the illustration (which includes a scale) the anteroposterior length of the midline appears to be 33mm, which falls within the range of Sumatran cave specimens of the third deciduous molar of *D. sumatrensis*, 30-41 mm, and below the range of *R. sondaicus*, 40-41 mm, from this source (Hooijer, 1946a). The transverse breadth of the tooth. however, also appears to be c. 33 mm, so that it is more nearly square in cross section than most of Hooijer's specimens (his 905 j being the exception, see loc. cit., p. 25). Unfortunately, the present location of the specimen is not known (D. W. McCredie, pers. comm., 1982), so that it is not possible to check these dimensions in the hand. It must be questionable whether use of the trinomial is justified in the circumstances.

3. Right lower third deciduous molar. Trench US/17, from surface 30-36 inches, Lobang Angus mouth, Niah cave, Sarawak. Sarawak Museum; unregistered.

An unerupted tooth, reported by Medway (1967:214). Associated artifacts at this level included bone tools of types that, in the West Mouth, occurred alongside the Mesolithic flake culture dated to the period c. 30,600 - c. 17,600 B.C.

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4.a & b Left upper first (?) permanent molar and right upper second (?) permanent molar.

Everett collection, British Museum (Nat. Hist.), reg. no. M 1968. Plate 3(a). See also Medway (1965, Plate xxi).

One molar is relatively more worn than the second, with respective crown heights (labial face) of 42.5 mm and 50 mm. If both are from the same animal, this difference in wear could probably be accounted for by different positions in the toothrow; on this basis, I have tentatively identified one as a first, the other as a second molar. In general appearance the teeth are similar, darkly coloured and slightly mineralised. The tooth roots are lost. Both show two characters diagnostic of the species: a distinct protocone fold (discernible on Plate 3, a), and the postsinus nearly as deep as the medisinus.

Measurements are given in Tables 3 and 4. The discrepancies in anteroposterior length between these and Hooijer's (1946a) values I attribute to differences in technique. As noted above, the biconvex sides of the labial face of this tooth make it difficult to select a consistent point for measurement to represent the 'crown base'.

				Antero-p	osterior length	Bread	ith	
Tooth	Age	Location	Reg. no./ Reference	Max.	Crown base	Antero- transverse	Postero- transverse	Species
(?)M ¹	Fossil	Sarawak	M.1968	48	44.5	51.5	48.6	D. sumatrensis
`́м!	Recent	Borneo	Groves (1967)	-	-	48.7±1.2	43.2+2.7	••
M,	Recent	S.E. Asia	Hooijer (1946a)	-	33-40	48-53	44-49	,,
M ¹ M ¹	Recent	S.E. Asia	Hooijer (1946a)	-	35-43	51.60	45-52	R. sondaicus
$(?)M_{2}^{2}$	Fossil	Sarawak	M.1968	50	46.5	50	46.6	D. sumatrensis
M_2^2	Recent	Borneo	Groves (1967)	-	-	49.3 <u>+</u> 1.4	-	,,
M ² M ² M ²	Recent	S.E. Asia	Hooijer (1946a)	-	39-41	48-52	43-49	"
M ²	Recent	S.E. Asia	Hooijer (1946a)	-	37-46	53-60	45-52	R. sondaicus
M ³	Fossil	Sarawak	M.4514		52	41.5	-	D. sumatrensis
м ³	Recent	Borneo	Groves (1967)		•	42.8+2.4	-	.,
М3	Recent	S.E. Asia	Hooijer (1946a)	-	52	45-47	-	••
M ³	Recent	S.E. Asia	Hooijer (1946a)	-	45-58	43-54		R. sondaicus

Measurements of upper molars of fossil and recent rhinoceroses, in mm; terminology follows Hooijer (1946a).

Table 3

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Measurements of lower molars of fossil and recent rhinoceroses, in mm. Terminology follows Hooijer (1946a).

Tooth	Age	Location	Reg. no./ Reference	A/p length	Transverse Ant. Post.	Species
P ₃	Fossil	Sarawak	M.1968	30.5	18.2 20.0	D. sumatrensis
P ₃	Fossil	Sarawak	M.4154	30.5	21.2 22.3	,,
P ₃	Recent	Borneo	Groves (1967)	29 .7±2.7	17.2+1.5	*7
P ₃	Recent	S.E. Asia	Hooijer (1946a)	27-31	19-22	**
P ₄	Fossil	Sarawak	M.1968	34.3	21.5 23.7	**
P ₄	Recent	Borneo	Groves (1967)	32.0 <u>+</u> 2.9	20.9±1.7	**
P ₄	Recent	S.E. Asia	Hooij <mark>er (1946</mark> a)	32-33	22	,,
(?) M ₁	Fossil	Sarawak	M.1968	36.4	23.0 24.5	••
M ₁	Recent	Borneo	Groves (1967)	38.5 <u>+</u> 3.7	24.1 <u>+</u> 1.3	••
M ₁	Recent	S.E. Asia	Hooijer (1946a)	36-41	24-26	**
M ₁	Recent	?	BM1948.12.20.1	43.1	25.4 27.5	**
(?) $M_{1/2}$	Fossil	Sarawak	M.4154	43.2	27.5 26.9	**
M ₂	Recent	Borneo	Groves (1967)	40.0 + 3.2	25.1±1.8	,,
M2 ²	Recent	S.E. Asia	Hooijer (1946a)	37-42	23-26	••
M ₁	Recent	S.E. Asia	Hooijer (1946a)	40-43	26-31	R. sondaicus
M ₁	Recent	Java	Groves (1967)	41.9±1.9	28.1±2.1	**

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In breadth, both teeth slightly exceed the mean values of recent specimens from Borneo; with the presumed M^1 more than 2 x s. d. greater but the M^2 within 1 s. d. Neither tooth, however, is outside the range of Hooijer's (1946a) recent sample from various locations, and both fall below the mean dimensions of recent homologues from mainland continental south-east Asia tabulated by Groves (1967).

5. Right upper third molar. Everett collection, British Museum (Nat, Hist), reg. no M 4154. Plate 3 (b).

This tooth is also darkly coloured and apparently slightly mineralised. It is moderately worn, with a crown height of 41mm on the labial face. In antero-transverse breadth it is smaller than the mean of 4 recent Bornean examples measured by Groves (1967), although within 1 s. d.; it is also below the range of the recent samples of both species measured by Hooijer (1946a). There can be no grounds for doubt about its identification.

6 - 8. Right lower third and fourth premolars and first permanent molar. Everett collection, British Museum (Nat. Hist.); reg. no. M 1968. Plate 4 (a).

These teeth are brown in colour, paler on the occlusal margins of the enamel ridges. They fit exactly to form a set, undoubtedly from one individual. Measurements are given in Table 4.

In anteroposterior length, these teeth all fall within 1 s. d. of the mean samples of recent D. sumatrensis from Borneo measured by Groves. In this dimension, moreover, they are significantly smaller (i. e., > 2 s. d.) than the mean value for the Javan (typical) race of R. sondaicus, which has the smallest teeth among the three races recognised by Groves (1967). My measurements separated the breadths across the anterior and posterior lophs of the tooth. Hooijer and Groves did not make this distinction, but it can be accepted that both took the highest measured value. It thus appears that in this dimension the fourth premolar (only) falls above the range of Hoojier's sample and between 1 s. d. and 2 s. d. above Groves's mean. The two other teeth are within indicated normal variation. Nonetheless, all values fall below the range of variation in breadth in the large sample of *R*. sondaicus measured by Hooijer.

Although there are no known features of dental anatomy that serve to distinguish the two species, their measurements leave no doubt that these teeth of the lower jaw are correctly attributed to *D. sumatrensis*.

9. Left lower third premolar. Everett collection, British Museum (Nat. Hist.); reg. no. M 4154. Plate 3 (b). Table 4.

The measurements of this tooth indicate a further increase in variability in the transverse dimension, but do not permit any identification other than *D. sumatrensis*.

10. Right lower first or second molar. Everett collection, British Museum (Nat. Hist.), reg. no. M 4154. Plate 3 (b). Table 4.

As Hooijer (1946a : 33) has pointed out, the first and second lower molars are so similar to each other that the serial position of isolated examples cannot be determined with certainty from appearance. The second lower molar of *D. sumatrensis* overlaps in dimensions with the first of *R. sondaicus* (Table 4), and this particular tooth could be assigned to either species. It is, however, no larger than M_1 , of BM. 1948. 12.20.1, from the Rothschild collection (without locality). Accepting that all positively identified associated teeth and post-cranial remains in this collection are *D. sumatrensis*, I feel justified in assigning this tooth to the same species.

B. Postcranial skeleton

In the following paragraphs, I treat the material from the Everett collection in an order which is based partly on registration number, but more on the need to develop the argument for specific identification. As already noted (above), an itemised inventory of the collection is given as Appendix I.

11. Proximal head and part shaft of left radius. Everett collection, British Museum (Nat. Hist.), reg. no. M 1969. Plate 4 (b), Table 5.

This bone, like all bones of the Everett collection, is brown in colour. It is rather heavily abraded around the margins, so that much of the natural sculpturing of the articular surface has been lost. Since these bones were presumably obtained by Everett from the gold workings near Bau, the source of most of his material, they are likely to have been subjected to rough treatment including seiving and washing, which would explain their present condition. As a consequer , accurate measurements cannot be taken. But, despite the wear through abrasion, the present dimensions of the head $(71.5 \times 50 \text{ mm})$ and of the shaft (35 mm) in lateral diameter) fall in the range of recent *D. sumatrensis* and well below that of *R. sondaicus* (Table 5).

12. Entire left radius. Everett collection, reg. no. M 4154. Table 5.

Again, although both proximal and distal heads are abraded and measurements consequently affected, the degree of loss is not enough to bring the values for the breadth of proximal and distal head into the range of R. sondaicus (Table 5).

The length of this radius exceeds the maximum measured among recent specimens. Among Bornean examples the radius of H 6381 measures only 288 mm but, since its epiphyses are not closed (see above). this bone had clearly not reached final, adult size, and I have excluded it from the tabulation; the only adult length known is 305 mm. for a specimen in Munich (measurement kindly supplied by Dr. C. P. Groves, *in litt.*, 1982). The archaeological specimen is thus some 6% longer than the longest radius of *D. sumatrensis* measured, and some 10% longer than the one available adult example of the Bornean subspecies, *D. sumatrensis harrissoni*, the smallest race of Sumatran rhinoceros (Groves, 1965, 1967. Groves & Kurt, 1972). As will be seen from further examples given below, this size difference is entirely in keeping with other skeletal elements in the Everett collection.

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Table 5

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Measurements, in mm, of the radii of recent and fossil rhinoceroses.

Species	Reg. no./ Reference	Breadth prox. head	Breadth distal head	Shaft length	Shaft diameter	Shaft diam./ length ratio
). sumatrensis	M.1969	71.5			35	
"	M.4154	84	84	336	45.5	.135
,,	BM(NH) Recent	76-78		295-318	32-42	.111132 ⁽¹⁾
R. sondaic us	Hooijer (1946a) + BM(NH) recent	107-111	90 - 93	318-349	44-56	.137170 ⁽¹⁾
D. sumatrensis	Niah (Burial no. 27)	83.7	(87)(2)	(350)(2)	(51)(2)	.146
	Adjusted values	83.7	85	345	48	.139

*Footnote:

(1) Ratios calculated for individual specimens.

(2) Measurements affected by damage to the specimen.

13. Right radius. The "pillow" in Mesolithic burial No. 27, West mouth. Niah Cave. Sarawak Museum (unregistered). Table 5, Plate 5.

In previous publications (for instance, Medway, 1965). I have attributed this bone to D. sumatrensis despite the fact that its length greatly exceeds any measured radius of recent specimens of this species of rhinoceros. Although the identification was not questioned by Groves and Kurt (1972), now that the presence of the larger R. sondaicus in prehistoric Borneo is demonstrated by the tooth from Madai caves, (no. 1, above) it is necessary to make a critical reappraisal

The bone was crushed and broken in situ. To protect and preserve it during and after recovery, the excavators coated it liberally with shellac. This hard covering has not been removed. The proximal head is undamaged, but the shaft has been broken a short way below (distad) to it. As a consequence, the proximal head is bent forward, i.e., anteriorad, with respect to the true axis of the shaft. As an effect of this flexure, the posterior median prominence is swung into an axial position and the total (median) length of the bone (350 mm; see Table 5) is obligatorily measured from the tip of this prominence. It appears to me that the breakage and consequent flexure of this bone may have increased its apparent length by a small amount, perhaps 5 mm. Below the neck of the proximal (humeral) articulation, the shaft is crushed and fragmented, laterally expanded and dorsoventrally flattened. The measurement of mid-shaft breadth (51 mm; see Table 5) is undoubtedly greater than the original diameter of the shaft. The distal head has been partly crushed: the maximum breadth seems not to have been badly affected, but the anteroposterior breadth may have been reduced.

Measuremens are given in Table 5. As noted, the breadth of the proximal head is not affected by damage in this dimension; the Niah radius is very close to the larger of Everett's specimens, and well below the range of recent R. sondaicus. The proximal anteroposterior diameter (50 mm) is also below the range for R. sondaicus (53 - 64 mm; see Hooijer, 1946a, p. 68). The short unbroken, uncrushed length of shaft below the proximal head measures only 50 mm in diameter. Since this is not the narrowest point of the shaft of an intact radius, the mid-length measurement of 51 mm (see Table 5) is certainly unduly high as a consequence of flattening and crushing; the true value is likely to have been not above 48 mm. The breadth of the distal head is also affected by damage, and it is reasonable to deduct at least 2 mm in adjusting this value (see Table 5). The anteroposterior measurement, also affected by flattening, is 49 mm (cf. 57-61 for *R. sondaicus*; see Hooijer, 1946a).

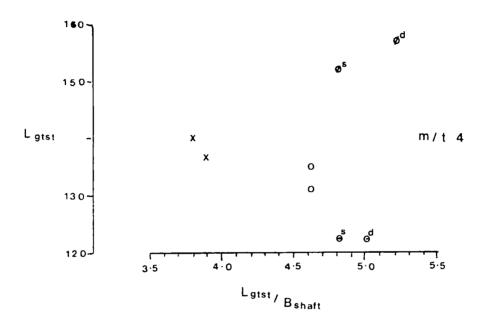
As shown in Table 5, the actual ratio of shaft diameter to length, at 146, is well outside the range for D. sumatrensis. The adjusted measurements give a lower ratio, which may still be artificially elevated. The character that confirms identification as an elongated D. sumatrensis is again the slenderness of the articular heads which fall well below the range of extant R. sondaicus. There can be no doubt that the animal that provided the Niah "pillow" radius was an exceptionally long-limbed Sumatran rhinoceros.

As noted above (pp. 7-8), the age of the specimen is conjectural, but probably falls between the date of 7800-13,000 B.C.

14. Right central (3rd) metacarpal. Everett collection, reg. no. M 1969. Plate 4 (b), Table 6, Figure 2.

15. Right central (3rd) metacarpal. Everett collection, reg. no. M 4154. Plate 6 (a) & (b), Table 6, Figure 2.

Of these two central metacarpals, one is slightly damaged and cannot provide a measurement of its greatest length. In median length, both fall well outside the range of recent D. sumatrensis, and even above the small sample of R. sondaicus. Yet both are comparatively slender. Measurements of the breadth of the distal articulating head and of the shaft breadth do not in fact exceed the range of recent D. sumatrensis and fall below the range of R. sondaicus. Their relative slenderness is emphasised by the ratio median length: shaft diameter. Values for this ratio among these fossil specimens fall entirely within the variation of recent D. sumatrensis, and well outside the limits of R. sondaicus. The difference in general proportion is clearly seen in Plate 6(b).



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Figure 2.

Length and relative breadth of right 3rd metacarpals of *Rhinoceros* sondaicus and Dicerorhinus sumatrensis.

Length and relative breadth of right 3rd metacarpals of *Rhinoceros sondaicus* (x) and *Dicerorhinus sumatrensis* (o) recent, including (o) from Borneo; fossil (\emptyset).

 L_{gtst} = greatest length in mm; ^Bshaft = shaft breadth at midlength.

s = (sin.), i.e., left; d = (dext.), i.e., right

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Measurements (in mm, to the nearest 0.5 mm) of third (central) metacarpals among Everett's specimens, compared with recent Dicerorhinus sumatrensis and Rhinoceros sondaicus (see Plate 6,b).

	Greatest length	Median length	Breadth of distal head	Greatest shaft breadth	Ratio (2) : (4)
	(1)	(2)	(3)	(4)	
) Everett collection					
M.4154 (right)	199	185	50	50	3.7
M.1969 (right)	-	165	43.5	47.5	3.5
) D. sum atrensis					
É H6381	160	149	39.5	38	3.9
1948.12.20.1	175	159	46.5	45.5	3.5
31.5.28.1	172	158	44.5	45	3.5
1949.1.11.1	175	158	47	49	3.2
94.9.24.1	173	157	47.5	50.5	3.1
Average	171.0	156.2	45.0	45.6	3.4
c) R. sondaicus					
723f	184	165	56.5	61	2.7
21.5.15.1	191	175	52	59.5	2.9

N.B. Among recent specimens, only H6381 originated from Borneo (Sarawak).

16. Right external (4th) metacarpal. Everett collection, reg. no. M 4154. Plate 6 (a), Table 7, Figure 3.

This foot bone is much longer than its homologues in the sample of recent D. sumatrensis, and also exceeds the two available examples of R. sondaicus. Yet it is comparatively slender, and in relative thickness nearer to D. sumatrensis than R. sondaicus (Table 7, Figure 3).

17. Right external (4th) metatarsal. Everett collection, reg. no. M 4154. Plate 7(a) & (b), Table 8, Figure 4.

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18. Left external (4th) metatarsal. Everett collection, reg. no. M 4154. Plate 7 (a), Table 8, Figure 4.

These bones of the hind foot repeat the features of those of the forefoot, i. e. although longer than homologues in recent skeletons of both rhinoceros species, they are identifiable as D. sumatrensis by their comparative slenderness (Table 8). In fact, since the mid-shaft diameter actually falls within the range of the shorter metatarsals of recent D. sumatrensis. the ratio is high, i.e., the bones more markedly slender in proportion to their length. As plate 7(b) shows, the two species are also distinguished by nonmetrical features – notably the shape of the proximal head, the curvature of the long axis of the bone and the development of a longitudinal flange on the median aspect.

There is a 3.3% difference in length and 3.2% difference in diameter between the right and left fossil metatarsals. Those of the right and left feet of H6381 are identical in both dimensions (Table 8), suggesting that the fossil specimens originated from two different individuals.

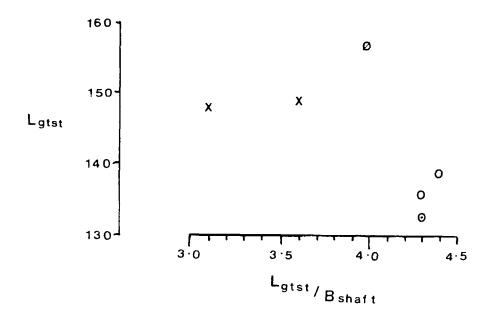
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Table 7

Measurements (in mm) of the fourth (external) metacarpal: Everett's specimen and recent rhinoceroses (see Plate 7, b).

		Greatest length	Median length	Breadth of distal head	Shaft breadth	Ratio (2) : (4)
		(1)	(2)	(3)	(4)	
a)	Everett collection M.4154 (right)	157	153	38.5	38.5	4.0
b)	D. sumatrensis H6381 1948.12.20.1 1949.1.11.1	133 139 136	129.5 135 133	31 36 37	30 30.5 31	4.3 4.4 4.3
	Average	136	132.5	32.7	30.5	4.3
c)	R. sondaicus 723f 21.5.15.1	148 149	143 144	47 42	45.5 40.5	3.1 3.6

Markey Construction (Structure Review)



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Figure 3.

Length and relative breadth of right 4th metacarpals of *Rhinoceros* sondaicus and *Dicerorhinus sumatrensis*. Conventions as in Fig. 2. $L_{gtst} = greatest length$.

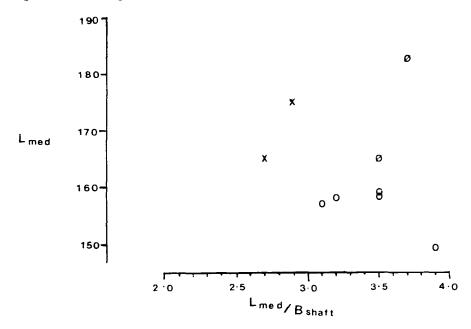


Figure 4.

Length and relative breadth of 4th metatarsals of *Rhinoceros* sondaicus and *Dicerorhinus sumatrensis*. Conventions as in Figs. 2 & 3.

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		Greatest length (1)	Breadth of distal head (2)	Shaft breadth (3)	Ratio (1): (3)
(e	Everett collection M.4154 (right) M.4154 (left)	157 152	32.5 31.5	30 31.5	5.2 4.8
(9	D. sumatrensis H6381 (right) H6381 (left) 1948.12.20.1 (right) 1949.1.11.1 (right)	122.5 122.5 135 131	27.8 27.8 32.5 31.5	24.5 25.5 29.5 28.5	5.0 4.6 4.6
	Average(1)	129.5	30.6	27.5	4.7
c)	R. sondaicus 723f (right) 21.5.15.1 (right)	140 136	36.5 33.5	37 35	3.8

(1) Footnote: Only the right metatarsal of H6381 is included in this average.

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19-22. Left and right calcaneum and astragalus. Everett collection. British Museum (Nat. Hist.). reg. no. M. 4154, Plate 8 (a), Tables 9 & 10.

The two fossil calcanea average 17% longer than the one available calcaneum of H 6381 of the small Bornean subspecies of *D. sumatrensis*, but do not attain the length of those in my sample of *R. sondaicus*. The breath across the lateral process is apparently not enlarged proportionally. The depth of the tuberous process, however. is proportionally greater than in recent *D. sumatrensis*, thus representing a condition more strongly divergent from *R. sondaicus*. This increased depth would presumably enlarge in proportion the area of attachment of the Achilles' tendon (*Tendo calcaneus*) implying that this longerlimbed, extinct form of D. sumatrensis was also provided with relatively powerful muscles of the lower leg.

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The measured dimensions of the two fossil astragalus again exceed values for recent D. sumatrensis. In this case, however, they do fall within the range of the small sample of R. sondaicus. Yet, since the two match their respective calcaneum in each case, there is no possibility of any other identification.

23. Left humerus, comprising distal head and part of shaft, 21 cm long. Everett collection, British Museum (Nat. Hist.), reg. no. M 4154. Table 11.

Once again, the fossil specimen is larger by some 20% in the measured dimensions when compared with H 6381, although it is only a fraction bigger than the largest humerus of *D. sumatrensis* from the general sample (Table 11). In both dimensions, it is well below the range of *R. sondaicus*.

The ratio of the chord of the lateral condyle to the breadth across the trochlea is more divergent from R. sondaicus than is the case in three of the sample of four recent D. sumatrensis (including H 6381). A longer arc of the distal articulation of humerus in the antero-posterior plane would reflect a comparatively greater length of the distal segments of the forelimb, once again indicating a longer-legged but proportionally slender form.

Table 10

	Max. breadth between outer condyles	Antero-posterior chord of lateral condyle
a) Everett collection		
M.4154 (right)	73.5	63.5
M.4154 (left)	74.5	63.5
b) D. sumatrensis		
H6381 (right)	56.8	52.3
H6381 (left)	57.5	52.3
76.711 (right)	70.5	59
1879.6.14.2 (left)	63	-
1949.1.11.1 (right)	65.5	60
1948.12.20.1 (right)	67.5	61
c) R. sondaicus		
723f (left)	72.5	66
21.5.15.1 (left)	72	59.5

Measurements (in mm) of astragalus : Everett's specimens and recent rhinoceroses.

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Table 11

Measurements (in mm.) of the distal head of a fragmentary left humerus in Everett's collection, compared with recent rhinoceroses.

	Breadth across condyles of trochlea	Lateral condyle (chord)	Ratio
a) Everett collection		(1)	
M.4154	84	81.5(1)	.97
b) D. sumatrensis			
H6381	69.7	64.5	.93
1948.12.20.1	82.5	75	.91
1879.6.14.2	71.5	70.5	.99
31.5.28.1	83.5	78	.92
c) R. sondaicus			
723f	101	90	.89
21.5.15.1	101.5	91.5	.90
Hooijer (1946a)	97-106	-	

Footnote: (1)Affected by abrasion

Table 9

Measurements of calcaneum, in mm: Everett's specimens and recent rhinoceroses.

		Greatest length	Depth of process (mid-length)	Depth/length ratio	Greatest breadth across lateral proces
a)	Everett collection				
ĺ.	M4154 (right)	113.5	55.5	.49	(65)(2) . (2)
	M4154 (left)	116	57	.49	· (2)
b)	D. sumatrensis				
,	H6831 (left)(1)	98	41.2	.42	58.5
	76.711 (right)	107	50	.47	69.5
	1879.6.14.2 (left)	99	46.5	.47	59
	1949.1.11.1 (right)	104	47	.45	68
	1948.12.20.1 (right)	107.5	49	.46	70.5
c)	R. sondaicus				
	723f (left)	125	52.5	.42	81.5
	21.5.15.1 (left)	136	53	.39	74

Footnote: (1) The catalogue shows that the right calcaneum of H6831 is missing. (2) The lateral process has suffered damage, most severely on the left calcaneum, affecting measurements.

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The following items of appendicular skeleton from the Everett collection are all confidently assigned to *Dicerorhinus sumatrensis*. All are somewhat abraded. I have compared each bone with its counterpart in reference skeletons of both rhinoceros species, and I am satisfied that in general appearance all match *D. sumatrensis*. Such measurements as can be taken invariably exceed values for homologues in the skeleton of H 6381 and fall within the upper range, or slightly above, values for other recent *D. sumatrensis*, without attaining the size of R. sondaicus.

- 24. Proximal head and part shaft of left tibia, reg. no. M 4154.
- 25. Left patella, reg. no. M 4154.
- 26. Left cuboid, reg. no. M 4154.
- 27. Left scaphoid, reg. no. M 4154:
- 28. Right unciform, reg. no. M 4154.
- 29. Left magnum, reg. no. M 4154.

Finally, the following five specimens (30-34) of Everett's collection have not been positively identified but there are no grounds for assuming that they are other than *D. sumatrensis*.

30-32. Vertebrae, comprising one more or less complete cervical vertebra (M 4154) (Plate 8,b), one neural arch (M 4154) (Plate 8,b) one fragment showing the vertebarterial canal. i.e., another cervical vertebra (M. 1970) (Plate 8,b), and one indeterminate fragment (M. 1970).

33. A distal fragment of a lateral metapodial (M. 1970).

34. A fragment of scapula (M. 1969).

35. Left internal (2nd) metatarsal, damaged. West mouth, Niah cave, trench E/C2 at 24-48 inches depth. Sarawak Museum; unregistered.

The distal epiphysis is missing, and the specimen therefore attributed to a juvenile. Identification was due to D.A. Hooijer (see Medway, 1965, Table 1). Measurements: length 67 mm, greatest shaft diameter at mid-length 19mm.

36. Central (3rd) subterminal phalanx of pes. Lobang Angus mouth, Niah cave, Sarawak. Trench US/22, at 18-24 inches, associated with a 'Mesolithic' culture, rich in artifacts of bone (Medway, 1967). Sarawak Museum: unregistered. Plate 9(a).

Proximodistal length 27 mm, breadth 44.5 mm. These measurements fall within the range of recent D. sumatrensis in the B.M. (N.H.). p/d length 26-29 mm, breadth 44-49 mm (4 measured), and well below that of R. sondaicus.

37. Damaged left central (3rd) metacarpal. consisting of the proximal head and a portion of the shaft, 9 cm in length. Agop Sarapad, Madai caves. Trench L3, 10-15 cm below modern cave soil surface. Excavated by the Sabah Museum in 1980. Sabah Museum reg. MAD 2, L3, 10-15, see Plate 9(b).

The lateral margin of the shaft below the head has been gnawed by a small rodent (e.g. rat), and the posterior tuberosity of the head has also suffered damage. The only useful measurement that can be taken is a chord, somewhat diagonally, across the curve of the articulation. This dimension measures 57.5 mm, slightly above the range of 52-57 mm for the sample of *D. sumatrensis* in B.M. (N.H.), but well below the value for *R. sondaicus* of 66 mm. This specimen thus supports the evidence that both species of rhinoceros occurred contemporaneously in the vicinity of Madai some 10-8,000 years ago.

Dicerorhinus sumatrensis/Rhinoceros sondaicus indet.

To complete the catalogue, I list briefly archaeological specimens that cannot be identified with certainty, either because in isolation they provide no diagnostic features, or because they are too fragmentary, or are now lost and cannot be checked.

A. Dental material

1. A "rhino tooth", reported by T. & B. Harrisson (1971: 90), from 40-48 inches in Agop Atas mouth, Madai caves, Sabah. No other details published. Present whereabouts unknown.

The following were recorded from the West Mouth, Niah cave by Medway (1965, Table 1). All specimens were attributed to *D. sumatrensis*, at that time thought to be the only rhinoceros to occur in Borneo at any period. All teeth were fragmentary and although they cannot at the moment be found for checking it is doubtful that a re-examination would satisfactorily provide a specific identification for any one of them. All were retained in the unregistered, stored collections of the Sarawak Museum.

2. Fragment of cheek tooth, unerupted; trench E/G6, at 12-24 inches.

3. Fragmentary lower molar, worn; trench E/B3, 24-36 inches.

4. Fragmentary cheek tooth; D/E2, 24-48 inches.

5. Fragmentary lower molar, unerupted: E/W1, 30-33 inches.

6. Fragmentary lower molar, little worn: E/G1, 36-12 inches.

7. Fragmentary lower molar, unerupted; E/B5, 42-48 inches.

8. Fragmentary cheek tooth; E/G1, 48-60 inches.

9. Fragmentary cheek tooth: E/B1, 60-72 inches.

These depths in the West mouth correspond to C^{14} dated ages up to 30.673 ± 700 B.C. at 72 inches. There is evidence of human frequentation throughout this deposit, and rhinoceros remains are believed to represent the quarry of past human visitors.

		Arch. spec. length	D.s. harrissoni	Average D.s. sumatrensis	Average R. sondaicus
		(mm)	%	%	%
Radius	M 4154 Niah "pillow"	336 350	113(1) 117(1)	110 115	102 106
Metapo	dials 4th metac <mark>arpal</mark> (2)	157	118(4)	114	106
	3rd metacarpal(3)	185 165	124(4) 111(4)	117 104	109 97
	4th metatarsal(2)	157 152	128(4) 124(4)	118 114	114 110
Calcaneum		116	118(4)	111	89

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Table 12

Dicerorhinus sumatrensis: Lengths of archaeological specimens of limb bones compared with recent examples, expressed as percentages.

Footnotes: (1) Compared with the specimen in Munich (aged ad), 298 mm. (2) The greatest length. (3) The median length. (4) As compared with the Cambridge specimen (subadult), H 6381.

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B. Postcranial remains

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The following also derive from stratified deposits in excavations in the West mouth at Niah cave (see Medway, 1965, Table 1). All are in the unregistered collections of the Sarawak Museum, in the security store.

10. Fragmentary lateral proximal phalanx; E/C3, 0-24 inches. The specimen is split longitudinally, and no useful measurement can be taken.

11. Left central proximal phalanx, in two parts: E/C3 (A), 60-66 inches, and E/C(C), 48-60 inches (Medway, 1965, Table 1, items 12 and 14).

The two pieces fit along their anterior margins, but material is still missing from the posterior region of the bone. The following measurements are possible on the reassembled bone: breadth of proximal head 43.5 mm. proximodistal length 37 mm, breadth of distal head 40.5 mm.

One interesting specimen, already mentioned (above) is unique in being heavily mineralized:-

12. Right lateral (4th) metacarpal; E/W9, 6-12. Sarawak Museum; unregistered. Identified by Hooijer (see Medway, 1965).

Discussion

1. The presence of the Javan rhinoceros, *Rhinoceros sondaicus* in Borneo.

The controversy over the existence of R. sondaicus in Borneo has already been discussed. The question was thought by Rookmaaker (1977) to be indisputably resolved. The discovery at Madai caves of a tooth of the upper jaw, showing unambiguously every diagnostic character of this species, and dated by radiocarbon means to the Pleistocene-Holocene boundary, now materially alters the situation. It becomes reasonable to accept as an additional example of R. sondaicus the fragment of ulna. from a related stratum at Agop Sarapad. In this case, again, the unquantifiable, nonmetrical characters that contribute to the general appearance of the specimen support the identification. Other, even less distinctive post-cranial elements, among the material from Niah, can now also be given the same identification, previously withheld for lack of supporting evidence. With the advantage of radiometric dating of the Madai cave deposit we are thus able to confirm the presence of R. sondaicus in Borneo at least in the period 8-10,000 years B. C., with a range that included both the northeastern and northwestern parts of the island.

The critical tooth is slightly larger in most dimensions than its homologue in the extant subspecies of Java, R. s. sondaicus, from which the purported Bornean specimen "R. nasalis" is evidently indistinguishable.

It is in fact intermediate in size between those of the recent sample and the fossil examples from Sumatran caves, of unknown but presumed early Holocene age (Hooijer, 1949). As Hooijer (1946a, 1949) has shown, there has been a marked tendency towards evolutionary diminution in size among Southeast Asian populations of many mammals during the post-Pleistocene era. To find the same phenomenon in this species of rhinoceros in Borneo is not unexpected.

There remains the question of when it became extinct. Our archaeological material evidently brackets a comparatively short period of past time and can provide no answer. A parallel can be drawn with the tapir, *Tapirus indicus*, shown by discoveries at Niah to have been present from the late Upper Pleistocene until at least c.6000 B.C. For both the Javan rhinoceros and the tapir unconfirmed reports or poorly authenticated specimens exist, to suggest that the species survived in Borneo up to the early 19th century. Thereafter, the fate of both is totally unknown. Local hunters do not bother to distinguish between the two rhinoceroses, or even between rhino and tapir. Elsewhere (Medway, 1977a), I have suggested that possibly the last tapirs succumbed during the holocaust of rhino hunting that occurred in the late 1930s. Could this also be true of the Javan rhinoceros?

2. Evolution of the Sumatran rhinoceros, *Dicerorhinus sumatrensis*, in Borneo.

Although these archaeological discoveries have proved the existence of R. sondaicus in Borneo, re-examination of the teeth and bones collected by A.H. Everett in Sarawak- more than a century ago - has not found any further item referable to this species. The earlier identification of this material as *Rhinoceros sondaicus*, by Lydekker and others, was perhaps based simply on the assumption, then still current, that this species was the sole rhinoceros of Borneo.

Yet it is indisputable that in length the intact long bones (including the foot bones) fall outside the upper limits of recent D. sumatrensis and, in several cases, well into or even beyond the range of this dimension in R. sondaicus. The decisive characters, in rejecting the latter identification, are those already used by Hooijer (1946a), namely the relative proportions of these bones and, in particular, the breadths of the articular heads and the shafts. The identification of the radius "pillow" from burial no. 27 at Niah cave is based on the same criteria. Coupled with non-metrical characters (i.e., general appearance), the measurements show that these rhinos of the prehistoric period were as long in the limb as (or longer than) R. sondaicus but retained the comparative slenderness of D. sumatrensis. In fact, some figures suggest that the extinct form was proportionally more slender than the extant, which may be considered its more squat as well as smaller descendant.

The degree of diminution that has occurred is difficult to assess because samples are so small. Available measurements show that the existing Sumatran rhinoceros of Borneo is the smallest subspecies of D. sumatrensis (Groves, 1965, 1967; Groves & Kurt, 1972). Unfortunately, there are very few whole skeletons in existence in the museums of the world, and the only example in Britain is immature. Comparisons with this one specimen must inevitably be viewed cautiously. For the present, it can only be noted that the foot bones among Everett's specimens are 11 - 28% longer than their homologues in the skeleton of H 6381. and the radius is 13% longer than that of the aged adult skeleton in Munich museum; the Niah "pillow" radius is 17% longer than the Munich specimen. As expected, the difference is less by comparison with median values for the wider sample of larger subspecies of D. sumatrensis from other parts of Southeast Asia (Table 12). This degree of diminution is very similar to the 17-24% size difference between a small sample of the humerus of recent D. sumatrensis and a right humerus from a cave deposit in Sumatra, reported by Hooijer (1946a: 26-27). It appears that the evolutionary trend towards smaller body size or. at least, towards shorter limbs, has been prevalent on the island of Borneo as on Sumatra.

A change in size among the teeth is also discernible. Yet, while the teeth are larger than the mean values of recent homologues among D. sumatrensis harrissoni, few are outside the expected range of variation. The very small sample prevents a firm conclusion. but it appears possible that the diminution in tooth-size has been relatively less pronounced than that in the length of the limbs.

H.J.V. Sody thought that the larger, longer-limbed *D. sumatrensis* described from Sumatran caves by Hooijer ought to be distinguished as a 'phyletic' subspecies. He accordingly gave it the name *engenei* (Sody, 1946). By the same criteria, the extinct Bornean population could also be considered taxonomically distinct from the recent population. The existing Borneo population has already been separated from all others of Southeast Asia, under the subspecific name *harrissoni* (Groves, 1965). The extinct Bornean population must be considered ancestral to *harrissoni*. Morphologically, the two show a relationship similar to that of *eugen* to typical *sumatrensis*. Both extinct populations consisted of individuals which were larger than their recent descendants.

Lowered sea levels of the last Pleistocene ice age would very probably have joined the existing large islands of the Sunda shelf, with the Malay Peninsula, into one continuous landmass. This would presumably have been inhabited by a single interbreeding population of *Dicerorhinus sumatrensis*. A Pleistocene/Holocene transitional date is applicable to the Niah radius (and, by inference, to Everett's specimens). By this period, rising sea levels may have interposed a barrier between the western and eastern parts of the Sunda shelf. The Sumatran and Bornean populations would therefore have been isolated, and may have begun to diverge morphologically.

The Bornean post-cranial remains are much more numerous than those from Sumatran caves, where dental material was obtained in greater richness. Comparisons are therefore difficult. It appears that during the post-Pleistocene period, selective pressure, operating apparently over no more than 10,000 years or so, has led to a reduction in linear dimensions of up to c. 20% in both populations. It can only be conjectured at what stage the differences between them were sufficient to warrant taxonomic separation. The chronological age of the Niah radius is known only within very wide limits: for the cave specimens from Sumatra and Everett's from Sarawak no date can be given. While the fossil material from Borneo is palpably separable from *D. s. harrissoni*, its relationship with *D. s. eugenei* is more obscure. At present, it seems inadvisable to apply any subspecific name.

3. Palaeoecological conclusions.

Neither Hooijer's Sumatran cave material nor that of the Everett collection were recovered from an organised archaeological excavation. It is unlikely that a date for either can now be established. If radiometric or other appropriate techniques are applicable, the result would produce an interesting case of a timed evolutionary change, a so-called "chronocline".

The appearance of the Everett specimens does not suggest that they are very different in age from the range of dates proven at Madai or at Niah. As noted, the bones are dark brown in colour, presumably as a result of staining in a cave earth, but they are not mineralised to a significant degree. Like the Sumatran fossils, they can reasonably be attributed to a date of terminal Upper Pleistocene to Holocene range, which would include the radiometric dates established for the Madai and Niah specimens.

This means that we can conclude, with reasonable certainty, that 8-10 thousand years ago there existed in Borneo a population of *Rhinoceros sondaicus* scarcely, if at all, larger than the present day form on Java, together with a population of *Dicerorhinus sumatrensis* averaging 10-20% taller but proportionally somewhat more slender than *D. s. harrissoni* of today. A third perissodactyl was also present: the tapir, *Tapirus indicus*. Two of these three during the subsequent millenia, became locally extinct while the third, through evolutionary processes, has undergone reduction in body size. To what cause do we attribute these changes?

Elsewhere (Medway, 1979) I have shown that the series of C^{14} dates taken from the cave deposit at Niah indicates accumulation rates in the range 2.2-3.1 inches (5.6 - 7.9 cm) per 1000 years. This is very slow by comparison with the accumulation rates of middle-type deposits attributed to human activity in the stone age in Iraq or Europe (Neanderthal man). I concluded that early stone age man was possibly rarer in Borneo than in these other environments. I also pointed out that the number of burials in the Neolithic cemetery, i. e., 127 over a 1200-year period, again suggested a very low population density. Early 19th century contacts with Borneo found small. scattered groups of people, concentrated in long-houses or villages alongside the principal waterways, and even smaller numbers of nomadic hunter-gatherers. At no past time is there evidence of a higher population density.

The existence of these specimens in the food middens at Madai and Niah of itself demonstrates that early man of that period was capable of catching and killing rhinoceroses and tapirs. But I find no grounds to suggest than man was so successful a hunter, or concentrated to such an extent on these large ungulates, that (prior to the use of shotguns) man can have had any significant effect as a predator upon these populations. We must therefore seek natural ecological factors that would, on the one hand, have selected progressively smaller *D.* sumatrensis, while also either exterminating *R. sondaicus* and *T. indicus* or at least reducing their populations to levels so low that they succumbed to hunting pressure very soon after the use of the shotgun became commonplace. Assuming that the ecological requirements of these three large ungulates are broadly similar, it appears that the post-Pleistocene environment has altered in a manner that has materially reduced the resources to which they are specifically adapted. One rhinoceros survived by the well-attested evolutionary response of reducing body size and so lessening the demands on resources made by each separate individual: the other may have followed suit but, starting from a larger initial size, was perhaps unable to adapt with the rapidity needed.

The history of the Southeast Asian tropical rainforest over this period is becoming known (Flenley, 1981). It seems clear that the post-glacial climatic amelioration. which permitted the rapid spread of tall rainforest, rich in giant, evergreen trees. must have produced a deteriorating environment for large perissodactyls.

In their present ranges, these rhinoceroses and the tapir feed chiefly by browsing (Groves, 1982). The plant species eaten are very variable; limited field data suggests that they favour vegetation characteristic of the forest edge, disturbed areas or second growth (Strickland, 1967; Hoogerwerf, 1970). Mature tropical rainforest supports a poor ground and shrub layer vegetation. Under the closed canopy, only a specialised flora survives. Growth is slow, sometimes with no more than a few leaves put on each year. The area of main primary productivity, the canopies of the tall trees, is out of reach. In short, it appears that mature, closecanopy rainforest is poor environment for rhinoceroses.

I conclude that these large ungulates were successfully adapted to the generally drier. somewhat cooler, and more seasonal, tropical environment such as prevailed in Sundaland during the last ice age. The onset of the warmer, less seasonal and perennially humid post-Pleistocene environment must have been marked by a resurgence of the rainforest. The present environment favours the growth of tree vegetation. Only river courses strike through the tall forest; with natural gaps caused by treefall, flood, landslides, etc., the riparian environment provides lush areas of highly productive, fast growing vegetation of low stature accessible to the large perissodacty l ungulates. Thus, as the postglacial environment developed to present-day conditions, the habitat suitable for large browsing ungulates must have diminshed progressively. Geographical isolation prevented immigration from the Asian continent. To such factors as these we must attribute the observed evolutionary change in Dicerorhinus sumatrensis and probably also the local extinction of Rhinoceros sondaicus in Borneo.

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Summary

The former presence in Borneo of the Javan rhinoceros, *Rhinoceros sondaicus*, is demonstrated by the identification of a left upper fourth deciduous molar, in unworn state, excavated from a layer radiometrically dated to the Pleistocene-Holocene boundary. Additional material attributed to this species is also identified from a midden at Madai, and stratified levels in the West mouth of Niah cave. Sarawak, all broadly contemporaneous.

Other material from Madai and Niah confirms that the Sumatran rhinoceros, *Dicerorhinus sumatrensis*, was also present throughout a longer period, from late Upper Pleistocene to recent dates. Metrical comparison, based chiefly on the collections made by A.H. Everett in Sarawak, indicates that this species has diminished in size by about 20% in the length of limb and foot bones during the Holocene. This size change is in accordance with trends observed generally among post-Pleistocene mammal species of the region. It is evident that there have been significant changes in the local environment, although the exact nature of these may remain uncertain.

Grateful thanks for assistance in the preparation of this paper go to Dr. Peter Bellwood, the late Mr. David William McCredie, Mr. Lucas Chin, The British Museum, (Natural History). Dr. Juliet Clutton-Brock, Dr. D.A. Hooijer, Miss E. Allen, Dr. X. Misonne and Dr. C.P. Groves.

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Appendix I

Inventory of rhinoceros specimens in the Everett collection. Department of Palaeontology. British Museum (Natural History).

M1968	Left upper 1st molar Right upper 1st or 2nd molar Right lower 3rd premolar Right lower 4th premolar Right lower 1st permanent molar
M1969	Proximal part of left radius Right central (3rd) metacarpal Fragment of scapula
M1970	Distal fragment of lateral metapodial Fragment of cervical vertebra Fragment of vertebra
M4154	Left lower 3rd premolar Right lower 1st (or 2nd) permanent molar Right upper 3rd molar Left radius Distal part of left humerus Proximal part of left tibia Left patella Left cuboid Left scaphoid Right unciform Left magnum Right calcaneum Right calcaneum Right astragalus Left astragalus Right lateral (4th) metatarsal Left lateral (4th) metatarsal Right central (3rd) metacarpal Right lateral (4th) metacarpal Broken cervical vertebra Neural arch and part centrum of (?) thoracic vertebra

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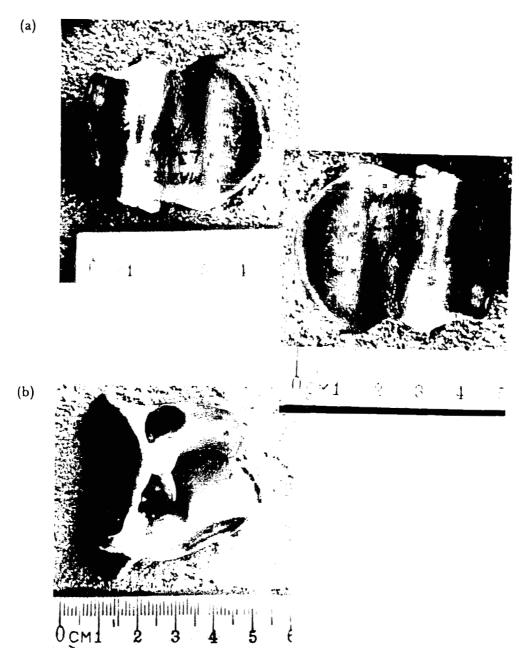
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 - (b) The proximal articular region of the right ulna of recent *Rhinoceros sondaicus*, to show the orientation of the Madai fragment.
- Plate 3. (a) Left upper first molar (*left*) and right upper second molar (*right*); M 1968, Everett Collection, British Museum (Nat. Hist.).
 - (b) Left lower third premolar (left), right lower first molar (centre) and right upper third molar (right); M4154, Everett Collection, British Museum (Nat. Hist.).
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 - (b) Left third metacarpal of *Dicerorhinus sumatrensis* from Agop Sarapad, Madai caves, Sabah.

Plate 1.

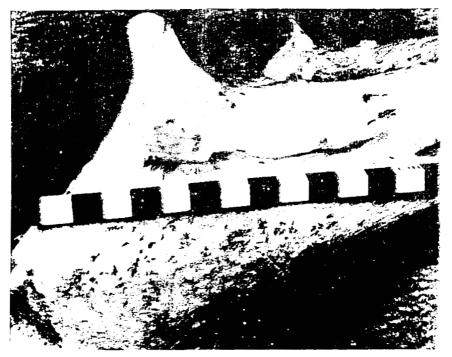


Left upper fourth deciduous molar of Rhinoceros sondaicus, Agop Sarapad, Madai caves, Sabah:

- (a) labial aspect;(b) occlusal aspect.



(a) The two fragments of right ulna (a.b.) of *Rhinoceros* sondaicus from Agop Sarapad. Madai caves, Sabah.



(b) The proximal articular region of the right ulna of recent *Rhinoceros sondaicus*, to show the orientation of the Madai fragment.





(b) Left lower third premolar (left). right lower first molar (centre) and right upper third molar (right);
 M 4154, Everett Collection, British Museum (Nat. Hist.).

Plate 4. andricus Deposits I E S,ER € M (a) Right lower third and fourth deciduous molars and first permanent molar. M 1968, Everett Collection, British Museum (Nat. Hist.).



(b) Right central metacarpal (above) and proximal part of left radius (below). M 1969, Everett Collection, British Museum (Nat. Hist.).

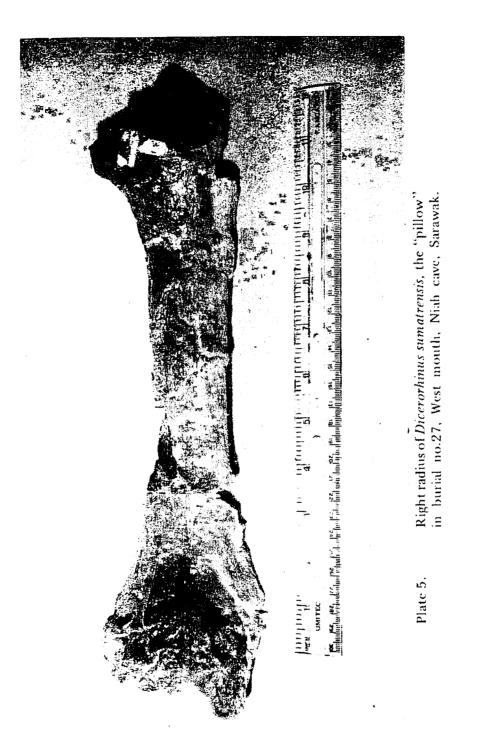
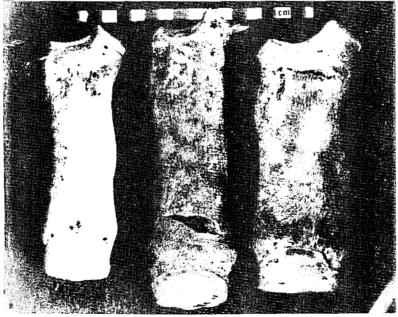


Plate 6.

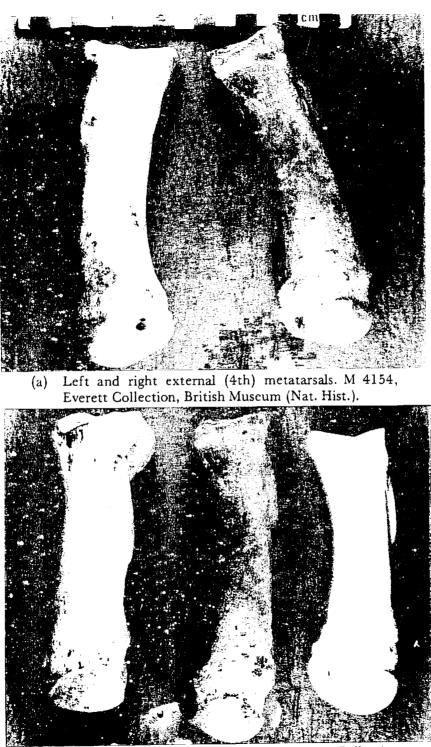


(a) Right central (3rd) metacarpal (left), right external (4th) metacarpal (centre) and right internal (2nd) metacarpal (right). All M 4154, Everett Collection, British Museum (Nat. Hist.).



(b) Right central (3rd) metacarpals of recent D. sumatrensis, BM 31.5.28.1 (left), from the Everett Collection, M 4154 (centre), and R. sondaicus, BM 723f (right).

Plate 7.



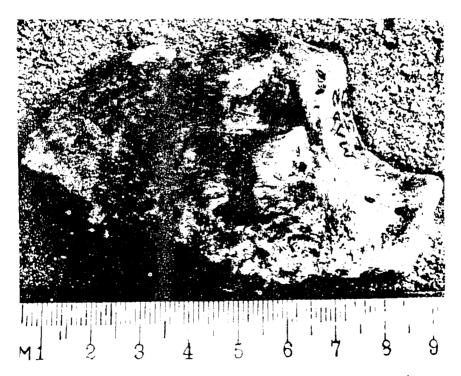
 (b) The right 4th metatarsal from the Everett Collection, M 4154 (centre), between its homologues from Rhinoceros sondaicus (left) and Dicerorhinus sumatrensis (right). 108

Plate 8. ć. Left and right astragalus and calcaneum, M 4154, Everett Collection, British Museum (Nat. Hist.). (a)

(b) Three damaged vertebrae; see text for identification. Everett Collection, British Museum (Nat. Hist.). Plate 9.



(a) Central (31d) subterminal phalanx of pes. Lobang Angus mouth, Niah caves. Sarawak Museum, unregistered.



(b) Left third metacarpal of Dicerorhinus sumatrensis from Agop Sarapad, Madai caves, Sabah.

