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THE SPECIES OF MUNTJAC (GENUS *MUNTJACUS*) IN BORNEO: UNRECOGNISED SYMPATRY IN TROPICAL DEER

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With 4 text-figures and 4 plates

ABSTRACT

The hypothesis, originated by Kohlbrenner (1895) and supported by Lyon (1911), Van Bemmelen (1952) and Hill (1960), that there are two taxonomically distinct muntjac (genus *Muntiacus* Rafinesque, 1815) on Borneo is supported by studies of abundant skin and skull material. The two are widely sympatric, so must rank as distinct species. One represents the widespread *M. muntjak* (Zimmermann, 1780) of southeast and south Asia, while the other is endemic. The type material of *Cervulus alihariensis* Kohlbrenner, 1895 consisted of a skin and frontal with antlers. As the skin has been lost, the frontal is designated as lectotype. It represents *M. muntjak*, as does the type of *M. rubidus* Lyon, 1911, so that the endemic species of Borneo is without a name. It is hereby designated *Muntiacus alihariensis*. The two species are diagnosed, described fully, and discussed.

INTRODUCTION

Valid species may go unrecognised once their names are reduced to synonymy. The case we describe below involves both the recognition of a controversial species and the resolution of an unfortunate nomenclatural confusion concerning it. The case is all the more exceptional in that it refers to species of deer — among the larger and so supposedly better known groups of mammals.

TAXONOMIC HISTORY

Kohlbrenner (1895) was the first to provide a scientific name for a muntjac from Borneo. During a journey through southeastern Borneo, he learned from the Malays that two species of muntjac inhabited the region: the "kidang merah" (red) and "kidang kuning" (yellow). From the Pleihari district he or his

PRESENT STUDY

collectors obtained several specimens of the former, which he assigned to the widespread southeast Asian species at that time known as *Cervulus muntjac*, but local people no example of the yellow species, although it was well known to the local people who said that its chief distinction aside from colour was the possession of simple, unbranched antlers. Eventually he managed to obtain, from a native merchant, a headless skin and a frontal with antlers, both corresponding to the natives' descriptions in that the skin was yellowish with a diffuse dark spinal stripe and the antlers were unbranched. On this basis, Kohlbrugge (1895: 192) named a new species, *Cervulus pletharicus*.

Eleven years later, in the course of describing a putative new species from Bangka, Lyon (1906: 583) referred again to *pletharicus*, noting that *Muntiacus Rafinesque*, 1815, antedates *Cervulus Blainville*, 1816, as the generic name for muntjac. He referred to *M. pletharicus* two skins and a frontal with antlers from Borneo, noting that the skins were distinctive, but the unbranched condition of the antlers could not be relied on, as an adult male from Tenasserim in the Smithsonian collection showed the same condition. Although he referred to Kohlbrugge's (1895) description, he did not comment on the latter's claim that two species of muntjac inhabit Borneo. Not long afterwards, however, he received specimens from Borneo which persuaded him that two species did indeed live there (Lyon, 1911: 71-75). Some specimens were referable to *M. pletharicus*, others to a new species *M. rubidus*, which was admittedly very close to the ordinary red muntjac from Bangka and elsewhere in southeast Asia. The antlers he had earlier assigned to *M. pletharicus* were now transferred to *M. rubidus*. Unbranched though they were, they were quite different from the tiny spike-like antlers characteristic of the yellow-coloured *M. pletharicus*.

Lyon's putative species *baranus* and *rubidus* together with *pletharicus* were reduced to subspecies rank under *Muntiacus muntjak* by Lydekker (1915: 15-16) and this view is still generally held today. Only Chasen (1940: 202-203) continued to list more than one species, keeping *M. pletharicus* separate from *M. muntjak*, but he admitted that it "seems to me to be a form of very doubtful validity", and it is difficult to believe that two species of the genus exist side by side in Borneo', though he had seen no material of *M. pletharicus*. Van Bemmel (1952: 17-20), in his revision of Sundaland *Muntiacus*, remained convinced of the distinctions between *pletharicus* and *rubidus*. Despite the evidence that they overlapped — he cited such evidence from Sarawak and from Klumpang Bay and Pamukang Bay — he continued to refer them both to subspecies of *M. muntjak*. Hill (1960: 107-108), on fresh material from the Robinson collection, confirmed the distinctions between the two as described half a century earlier by Lyon, but like Van Bemmel he regarded them as subspecies.

In his Sabah collection, Davis (1962) had only specimens referable to *pletharicus*, and on the basis of the comparative descriptions of the antlers he suggested that "*pletharicus*" was the young adult, "*rubidus*" the old adult of the male of the species. Following him, Medway (1965: 159; 1977: 149) united the two, making *rubidus* a synonym of the older name *pletharicus*.

From our studies it is quite clear that there are indeed two species of muntjac on Borneo, which differ in colour and in antler conformation. The red species is not represented by old males only: at all ages the antlers are larger and more robust than in the yellow species, so it is clear that they are not merely age stages. The red species is very close to the red muntjac of Java, Sumatra, Bangka and mainland southeast Asia and clearly conspecific. The yellow one must be specifically distinct, as it overlaps widely with the red species in Borneo and appears to have no close relatives elsewhere.

When skull and antler measurements are compared (table 1), the magnitude of the differences emerges: though skull sizes actually overlap, the antlers are invariably smaller in the yellow species, with small, thin pedicels.

TYPE MATERIAL OF *CERVULUS PLETHARICUS*

Kohlbrugge (1895: 192-194) described *Cervulus pletharicus* on the evidence of a frontal with antlers and a headless skin. He described the pedicels as being much longer and thinner than in "*Cervulus muntjac*" (as represented by his specimens referred to the Bornean red form) and the antlers shorter, thinner and straighter with no brow tine, these latter features being, he notes, the chief characteristic of the yellow species. Although such features characterise the young of *C. muntjac* as well according to Horsfield (1824), the *pletharicus* frontal must be adult according to Kohlbrugge, as (1) the sagittal suture is closed, whereas Horsfield describes his young specimen as having "the sutures very distinct in all parts and in several places the bones are still disunited"; (2) it has a well-developed burr, unlike the young specimen figured by Horsfield; and (3) its pedicels are longer than those of adult red muntjac, whereas in Horsfield's juvenile they were shorter and more slender.

Horsfield's juvenile is clearly only six months old or less. According to Van Bemmel (1952: 6) the first antlers in *Muntiacus* may consist of a transient "pair of small buds which are... soon shed and replaced by a pair of single-tined antlers", or may "attain a length of a couple of centimetres and are carried much longer. They may be replaced by a second pair of single-tined antlers or by a second set of four points (2 + 2)". The pedicels are more or less well-developed by the time the first antlers emerge. In any case, there are no grounds for assuming either that the *pletharicus* type frontal must be mature, or that simple burr-less spikes are the only antler type developed in immatures. As for the state of the sutures, it is all too easy to overlook how extremely early the sagittal suture closes during development in horned ungulates. The *pletharicus* antlers and their pedicels are far too large for a Bornean yellow muntjac, their measurements (pedicel length 117 mm, breadth 20; antler length 76, span 102) fitting well into our "subadult male" category for the red species. Moreover, on the left side there is an incipient basal tine.

The skull of the holotype of *rubidus* actually has smaller, less curved antlers than the type of *pleiharius* and, though brow tines are present, the burrs are weaker and much less rugose. The sagittal suture is more convoluted, suggesting that the specimen is a little older than the *pleiharius* type, but with poorly developed antlers.

The skin described by Kohlbrugge was said to be yellow-brown or orange-yellow instead of yellow red-brown as in *Cerulus munjiaq*, with a dark spinal stripe, whereas in *C. munjiaq* there is only a diffuse darkening; and the uppermost part of the limbs was orange-yellow rather than blackish brown. These characters certainly sound like a Bornean yellow munjiaq, but the skin has been lost so this cannot now be confirmed. Van Bemmelen (1952: 20) says that the type is a "skin and skull", but does not state that these were actually among the specimens he studied, besides which the "skull" is not in fact a complete skull, suggesting that Van Bemmelen did not see the specimens and that the skin might have been missing even then. Van Bemmelen's revision was essentially completed in Indonesia, on the Bogor collection alone. In any case, the skin if truly of the yellow species cannot belong with the frontlet. It is clear from Kohlbrugge's account that he had bought the headless skin and the frontlet with antlers from a native merchant, and that he just assumed they were of one and the same animal.

Consequently we here choose the frontlet with antlers (figured by Kohlbrugge (1895: fig. 1) and now registered as RMNH 28673 in the Leiden Museum) as the lectotype of *Cerulus pleiharius* Kohlbrugge, 1895, which makes this name a senior synonym of *Muntiacus rubidus* Lyon, 1911, and so unavailable for the Bornean yellow munjiaq.

THE BORNEAN SPECIES OF *MUNTIACUS*

Muntiacus munjiaq pleiharius (Kohlbrugge)

Bornean Red Munjiaq (figs. 1-3; pls. 2, 4)

- 1895 *Cerulus munjiaq*: Kohlbrugge, Natuurk. Tijdschr. Ned.-Indië, 55: 192, fig. 2. Pleihari, southeast Borneo.
 1895 *Cerulus pleiharius*: Kohlbrugge, loc. cit.: 192, fig. 1. Frontlet with antlers (lectotype). Pleihari.
 1911 *Muntiacus rubidus* Lyon, Proc. U.S. Nat. Mus., 40: 73. Pamukang Bay.
 1915 *Muntiacus munjiaq rubidus*: Lydekker, Cat. unguil. mamm. B. M., 4: 16 (in part).
 1940 *Muntiacus munjiaq rubidus*: Chasen, Bull. Raffles Mus., 15: 203.
 1952 *Muntiacus munjiaq rubidus*: Van Bemmelen, Beaufortia, 16: 17-19.
 1960 *Muntiacus munjiaq rubidus*: Hill, Bull. Raffles Mus., 29: 107-108.
 1965 *Muntiacus munjiaq pleiharius*: Medway, Mongr. Malay Branch Roy. Asiat. Soc., 7: 160 (in part).
 1977 *Muntiacus munjiaq pleiharius*: Medway, loc. cit., second ed.: 149 (in part).

Lectotype. — A frontlet with antlers, RMNH 28673, purchased by J. H. F. Kohlbrugge at Pleihari, southeast Kalimantan (Borneo) between 15th and 21st December 1894 (pl. 4 fig. c).

General diagnosis and description. — General colour dark reddish chestnut, almost maroon, slightly darker along dorsum with dark-tipped agouti hairs; an ashy suffusion ventrally; neck paler ventrally; interramal area and throat whitish grey or nearly pure white; inside of hams, underside of tail and groin white, sometimes extending as a stripe inside hind leg to level of hock, more usually pale brownish here; axilla and inside of forelimb down to carpus pale brownish; legs uniform grey-brown on outer surfaces; blaze and muzzle dark grey-brown; cheeks and above eyes dull orange-brown; frontal tufts prominent, very dark blackish brown, in males continuing as blackish stripes along pedicels, which are otherwise bright orange, a colour which extends to occiput and ear-bases, this one being sharply marked off from darker and duller tone of rest of head; ears chiefly dark grey-brown behind, white inside; a fine sprinkling of white hairs on upper lip and digits and lower limbs in some specimens.

Shoulder height recorded as 1030 and 1057 mm in two nearly adult males (BM 55.1002 and 55.1003), 978 and 1110 mm in two adult females (BM 55.1001 and 55.1004).

Skull (figs. 1-3; pl. 2 figs. a-c, pl. 4 figs. a-c) larger than in *M. atherodes*, averaging larger in most dimensions (greatest length of adult males 185-199 mm), deeper and more prognathous with somewhat less convex braincase in many specimens; frontal ridges more prominent in both sexes; preorbital pits shallower, less clearly demarcated along ventral rims, floor of pits always continuous with surface of jugal. Pedicels straighter, much thicker (18-29 mm), relatively more flattened laterally, much longer (64-149 mm). Antlers variable in development with age, attaining a much larger size (73-130 mm), deeply grooved, hooked inward and when fully mature having a discrete brow tine. A distinct burr in all adult antlers, indicating that antler shedding is usual.

Lyon (1911) listed a number of cranial characters whereby his sample of six "*pleiharius*" (i.e. *atherodes*) skulls differed from his sample of two "*rubidus*" (i.e. *pleiharius*), but with a more extensive series, most of these differences break down. In the yellow species the articulation of the upper extremity of the premaxilla with the nasal was said to be extensive instead of just a point contact; but specimens of red munjiaq that were unavailable to Lyon span the range of variation. The superior portion of the lacrimal, above the preorbital pit, was said to be much narrower in the yellow species; and although this is true if only the holotype of *rubidus* is considered, the contrast is less extreme when other red munjiaq skulls are examined and it does not apply at all to females. The anterior supero-external surface of the jugal was said to be narrower and more pointed in "*pleiharius*", but again some skulls of the red species approach this condition. A difference in "*rubidus*" in both sexes, because of the more prominent facial ridges, greater in "*rubidus*" in both sexes, because of the more prominent facial ridges. Hill (1960) states that no concavity at all is evident in "*pleiharius*", but in our much larger sample the difference appears to be more one of degree and some slight concavity is apparent in most skulls of the yellow munjiaq. Lyon stated that the arch over the posterior nares in "*pleiharius*" was marked by a definite

A. *Muntiacus atherodes*

Museum number	Locality: No. Place	a. Adult males					Antler length span
		Greatest length	Mastoid width	Pedicle l.	br.	Antler length span	
BN1 8.7.17.24	"N. Borneo"	183	49	—	—	—	—
BN1 71.3088	5 Tawau (TYPE)	192	56.5	82	11.5	29	81
FMNH 85904	6 Kalabakan	179	53	87	11	21	—
BM 95.5.7.6	41 B. Sekiwa	184.5	54	79	12	42.5	73.5
BN1 94.6.12.11	43 G. Mulu	189	58	—	—	—	—
BN1 95.5.7.5	45 S. Miri	188	56	—	—	—	—
BN1 55.1.005	33 Ulu Paku	185	52	88	13	35	81
ANINH 107116	28 Landak	201	57	67	10.5	33	—
AMNH 107118	28 Landak	177	51	75	10.5	27	—
AMNH 107119	28 Landak	184	52	65	11.5	27	—
NIZB 7499	28 Landak	180	55.5	86	—	16	61
NIZB 7496	28 Landak	180	54.5	83	—	26	63
USNM 153771	27 S. Kendawangan	183	55.5	69.5	10.5	21	92.5
USNM 196886	26 G. Talisayan	188	55	77	10.5	16	75.5
AMNH 106290	25 Riam	182	51	77	—	29	—
AMNH 103703	24 S. Cempaga	188	53	70	13.5	32	—
NIZB 7491	24 Pari Cempaga	176	51.5	78	—	20	44
USNM 151862	21 T. Kumpang	191	55.5	69	11.5	33	76
USNM 196884	16 B. Panggal	175	51.5	78	10.5	20	65
USNM 197692	14 Tanjung Seglu	182	52	72	12	31	77
USNM 198308	13 Medang	187.5	55	68	10	32.5	74

b. Subadult males

FMNH 68761	3 B. Kreiam	—	57.5	83	10.5	17	—
FMNH 68763	1 Sandakan	185	55	98	11.5	29	—
ANSP 7080	40 G. Dulit	188	52	91	11	20	—
BN1 55.1.006	33 Paku	—	—	ca. 85	11	29	66
MZB 7498	28 Landak	175	53	91	—	30	53
MZB 7493	25 Riam	174	53	73	—	—	—
ANINH 103704	24 S. Cempaga	187	58	104	12.5	33	—
USNM 154384	20 T. Pamulang	179	52	90	9.5	24.5	72.5
ANINH 103981	9 Peleban	185	53	80	9.5	22	—
ANINH 103980	9 Peleban	183	52	84	11	26	—

c. Adult females

USNM 34883/19161	1 Sandakan	192.5	53	—	—	—	—
FMNH 85905	6 Kalabakan	194	53	—	—	—	—
BM 89.1.8.8	41 B. Sekiwa	—	—	—	—	—	—
MZB 7494	29 Landak	186	57	—	—	—	—
USNM 197694	15 G. Menganne	181	50	—	—	—	—
ANINH 103749	7 Badang	178	49.5	—	—	—	—

d. Subadult females

FMNH 68764	2 Sandakan	184.5	53.5	—	—	—	—
FMNH 85903	6 Kalabakan	174	49	—	—	—	—
FMNH 88781	36 S. Sui	186	54.5	—	—	—	—
FMNH 88783	37 S. Buaya	177	52	—	—	—	—
MZB 7497	29 Landak	155	52	—	—	—	—
AMNH 106291	25 Riam	185	53	—	—	—	—
MZB 7492	25 Riam	174	51	—	—	—	—
USNM 197693	15 S. Menganne	187	53	—	—	—	—

B. *Muntiacus muntjak pliharicus*

Museum number	Locality: No. Place	a. Adult males					Antl length sp
		Greatest length	Mastoid width	Pedicle l.	br.	Antl length sp	
BM 93.3.4.10	46 Siprang	—	64	120	22	81	116
BM 2972.10.13	44 S. Baram	—	69.5	149	29	121	166
RMNH 29758	32 G. Kenepai	194	55	74	15	24	87
USNM 153767	27 S. Kendawangan	—	—	107	23	102	132
USNM 153768	27 S. Kendawangan	—	—	104	21	81	134
USNM 153756	27 S. Kendawangan	—	—	99	23	116	141
USNM 153757	27 S. Kendawangan	—	—	107	21	91	155
USNM 153758	27 S. Kendawangan	—	—	99	25	95	135
USNM 153759	27 S. Kendawangan	—	—	97	18	76	121
USNM 153760	27 S. Kendawangan	—	—	108	18	100	114
USNM 153761	27 S. Kendawangan	—	—	116	22.5	97	135
USNM 153762	27 S. Kendawangan	—	—	97	22.5	100	128
USNM 153763	27 S. Kendawangan	—	—	117	19	73	119
USNM 153764	27 S. Kendawangan	—	—	69	23	130	155
USNM 153765	27 S. Kendawangan	—	—	103	24.5	88	129
USNM 145365	49 Semandung	—	—	111	26	113	153
USNM 145366	49 Semandung	—	—	102	20	85	147
USNM 145368	49 Semandung	—	—	106	26	107.5	147
USNM 145367	50 S. Sempanjang	—	—	110	24	91	140
RMNH 29756	23 Pehari	—	—	—	24	117	151
USNM 151863	20 Pamulang Bay	197	61	111	21	75.5	112
USNM 154415	19 S. Paar	—	—	109	23	87	152
USNM 197691	11 B. Putih	—	—	113	—	77	107
AMNH 103748	7 Badang	189	61	72	21.5	86	—
RMNH 29753	"Borneo"	199	58	106	22	—	—

b. Subadult males

FMNH 88785	38 Ulu Selio	—	57	102	20	65	—
BM 99.12.9.83	40 G. Dulit	—	57	107	11	23	99
BM 55.1002	33 Ulu Paku	—	55	116	16.5	51	92
BM 55.1003	34 Anyut	—	62	107	18	86	101
RMNH 29760	32 G. Kenepai	174	53	113	12	—	83
RMNH 29761	32 G. Kenepai	169	51	96	12	—	70
RMNH 29757	32 G. Kenepai	194	55	74	15	24	87
RMNH 28673	23 Pehari (TYPE)	—	—	117	20	76	102

c. Adult females

BM 92.2.7.19	40 G. Dulit	174	—	—	—	—	—
FMNH 88786	38 Ulu Selio	190	55	—	—	—	—
BM 55.1001	34 Anyut	190	55	—	—	—	—
BM 55.1004	34 Anyut	188	56	—	—	—	—
USNM 198306	17 Samarinda	199	55	—	—	—	—
USNM 198307	12 S. Karang	209	60	—	—	—	—
MZB 1167	18 Long Petah	187	56.5	—	—	—	—
MZB 1168	18 Long Petah	182	56	—	—	—	—

76dext. 102

83sin.

ridge instead of being smooth and rounded, while Hill remarked that the lower edge of the mesopterygoid fossa was sharply pointed, not rounded. We find no really consistent difference, and much individual variation in both species. Finally Lyon also found that the interparietal was twice as wide as long in "*pletharicus*", but three times as wide as long in "*rubidus*". This appears to be a consistent difference, at least in males, a consequence of the more prominent lambdoid crest in the latter, and is true to an even greater degree for the closely related Bangka race.

Muntiacus atherodes sp. nov.

Bornean Yellow Muntjac (figs. 1-3; pls. 1, 3)

1895 *Cervulus pletharicus* Kohlbrugge, *Natuurk. Tijdschr. Ned.-Indië*, 55: 192. Plethari, southeast

Borneo. Skin only (see above).

1906 *Muntiacus pletharicus*: Lyon, *Proc. U.S. Nat. Mus.*, 31: 583, note a (skins only).

1911 *Muntiacus pletharicus*: Lyon, *Proc. U.S. Nat. Mus.*, 40: 71.

1915 *Muntiacus munjak pletharicus*: Lydekker, *Cat. unguil. mamm. B.M.*, 4: 16; *M. m. rubidus*, loc. cit.: 16-17 (in part).

1940 *Muntiacus pletharicus*: Chasen, *Bull. Raffles Mus.*, 15: 202-203.

1952 *Muntiacus munjak pletharicus*: Van Bemmelen, *Beaufortia*, 16: 19-20.

1960 *Muntiacus munjak pletharicus*: Hill, *Bull. Raffles Mus.*, 29: 103.

1962 *Muntiacus munjak pletharicus*: Davis, *Bull. Nat. Mus. Singapore*, 31: 123-124.

1965 *Muntiacus munjak pletharicus*: Medway, *Monogr. Malay. Branch Roy. Asiatic Soc.*, 7: 160

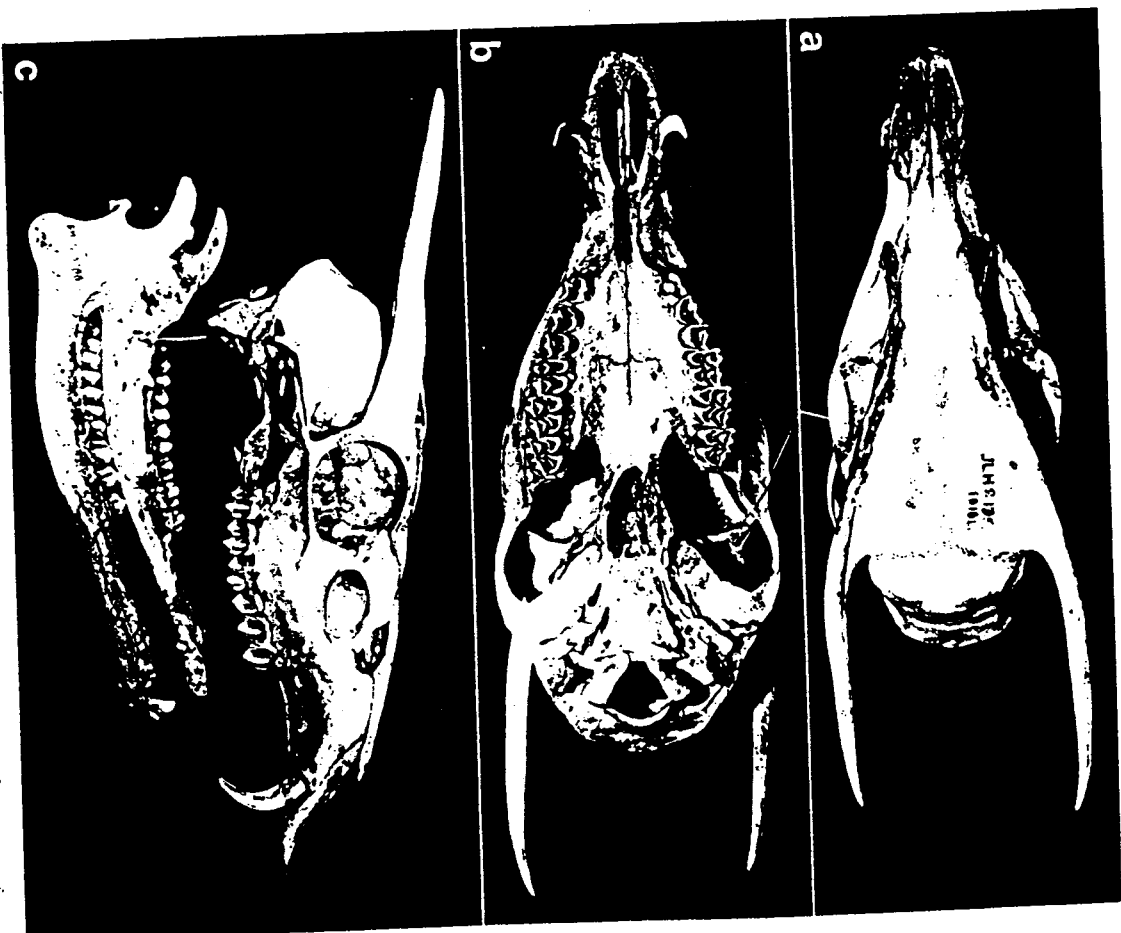
(in part).

1977 *Muntiacus munjak pletharicus*: Medway, loc. cit., second ed.: 149 (in part).

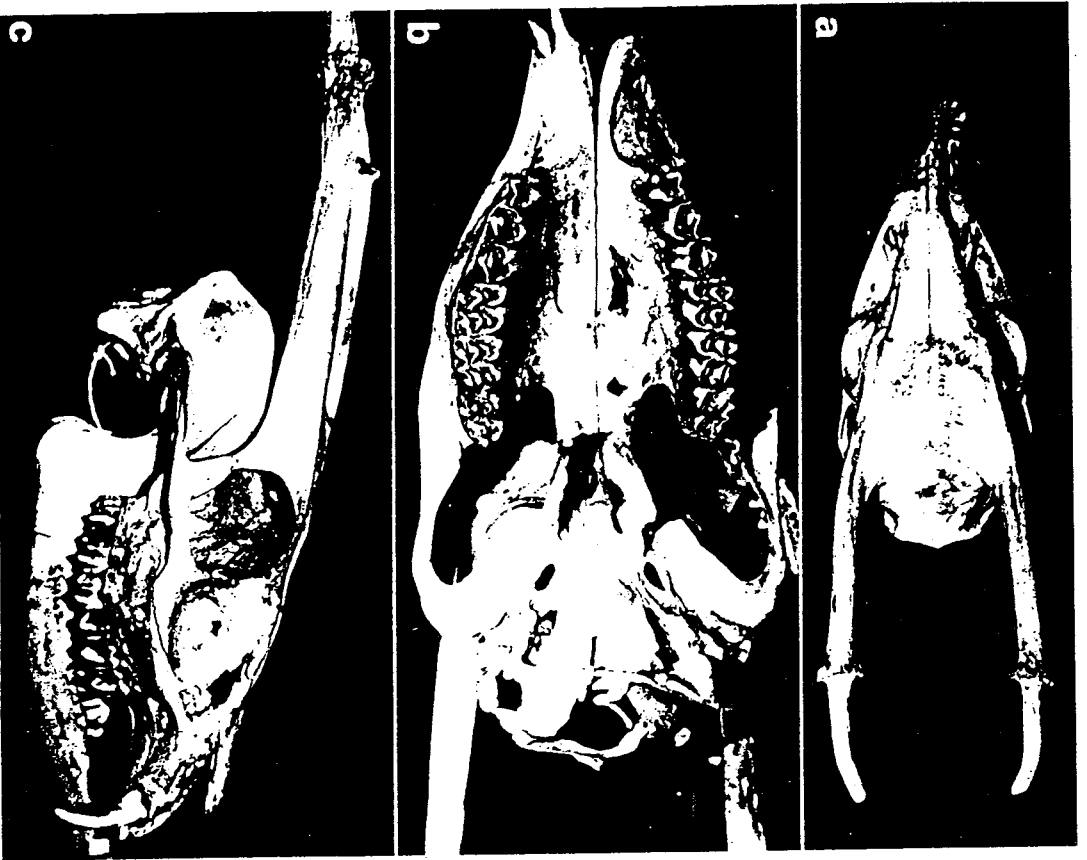
Holotype. — BM 71.3088, skin and skull of an adult male, from near forest camp 1, Cocoa Research Station, Tawau, Sabah, 800 ft. Collected by J. L. Harrison, 20th July 1962 (pl. 1 fig. a).

Diagnosis. — A species of *Muntiacus* differing from all others in the light orange-yellow general colour with dark diffuse dorsal stripe, lack of frontal tuft and tiny spike-like antlers on very short, slender pedicels.

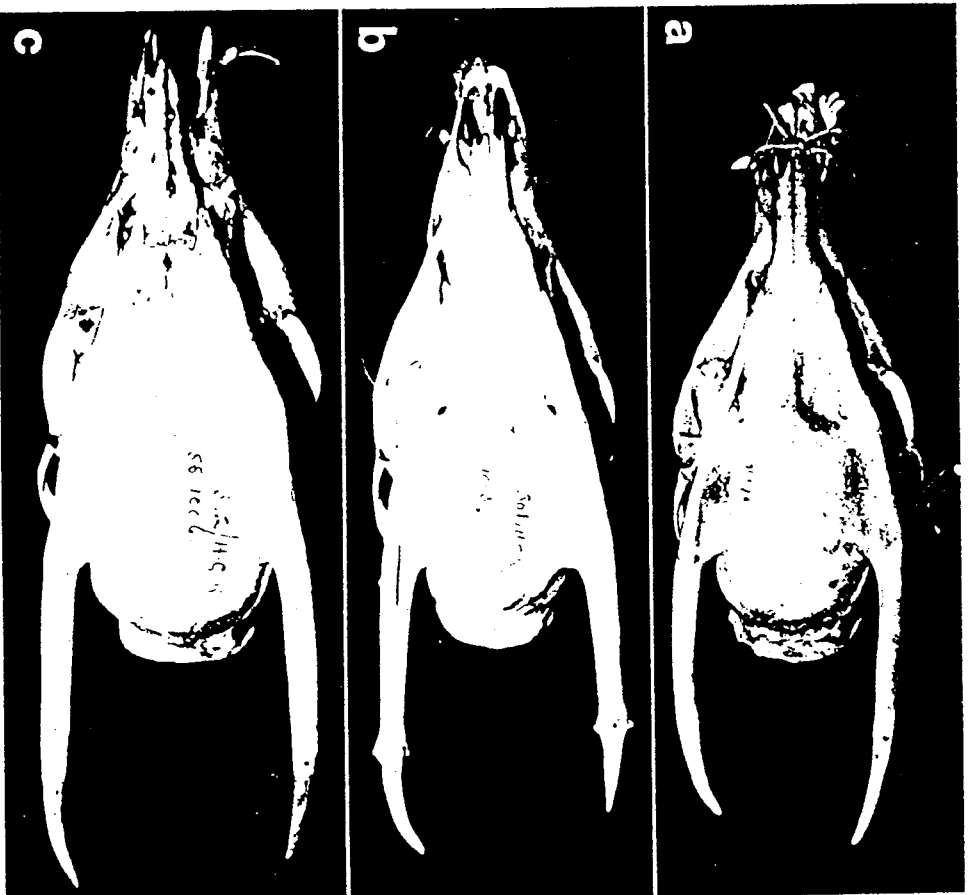
Description. — General colour bright ochraceous orange; more speckled (hairs with extensive black tips) in diffuse brownish stripe, about 15 cm broad, along dorsal midline; much paler and less speckled (fewer black-tipped hairs) on sides and legs. Tail usually dark brown above, white below. Belly pale orange-ochre, ventral surface of neck paler than body; throat and interramal region pale orange-ochre to nearly whitish; groin and inside of hams whitish; whitish down inside of leg to level of carpus or tarsus or as far as level of lateral hooves. Outer surface of legs coloured as body, but with light grey speckling on fronts of shanks in some specimens. Muzzle grey-ochre shading to pale brown of cheeks and to contrasting blackish brown of forehead, which tone continues across occiput into a well-marked narrow nuchal band, which in turn broadens into the more diffuse dorsal stripe. Dark forehead tone also continues onto dorsal surface of horn pedicels of males. Orange speckling between frontal glands, with blackish hairs bordering the glands themselves. Dark occipital area clearly marked off laterally by a light chestnut stripe above eyes continuing onto lower surface of pedicels of



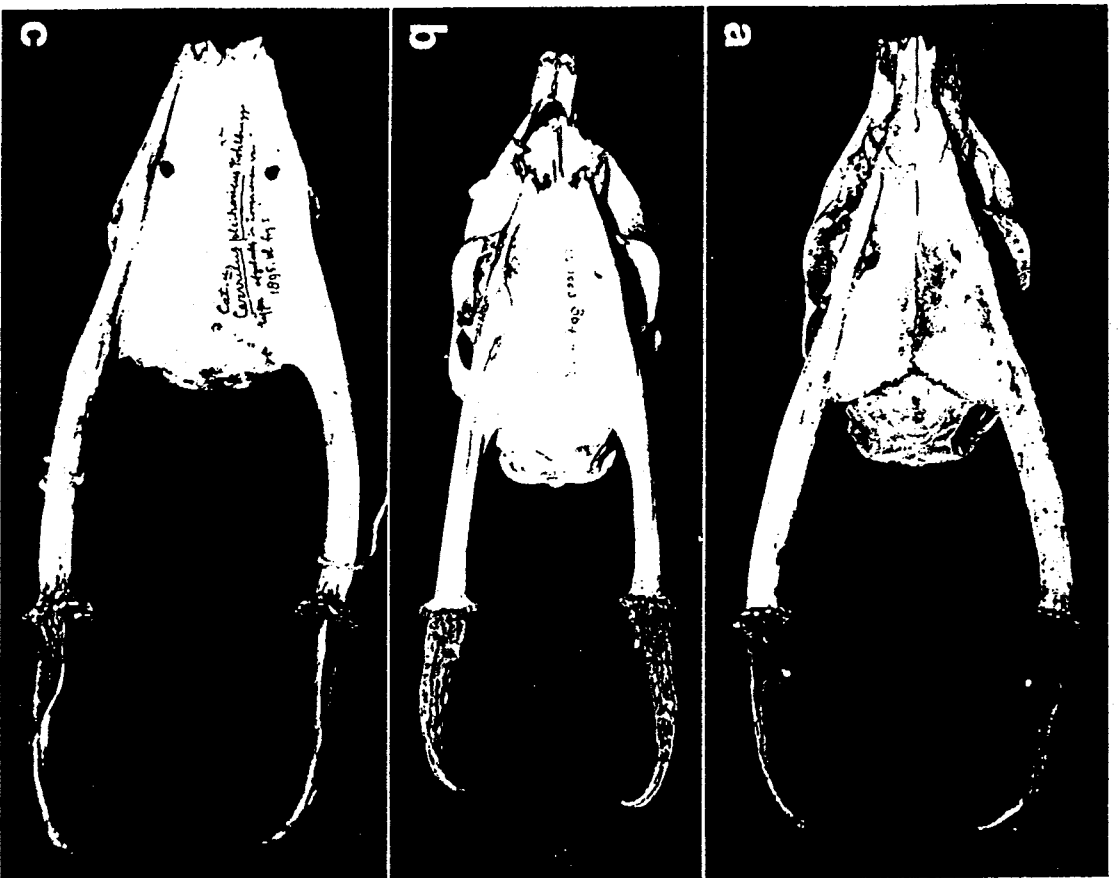
Skull of *Muntiacus atherodes* sp. nov., holotype, BM 71.3088, adult male from near forest camp 1, Cocoa Research Station, Tawau, Sabah. a) dorsal view; b) ventral view; c) lateral view.



Skull of *Mantidius munitiak philipponis*, BM 55.1002, young adult male. a) dorsal view; b) ventral view; c) lateral view.



Skulls of *Mantidius albertus* sp. nov., in dorsal view. a) BM 95.576, adult male; b) BM 55.1005, adult male; c) typical specimen with a small horn at base of antlers (BM 55.1006, young male).



Skulls of *Munitarius montiae pletharicus*, in dorsal view: a) BM 933410, adult male; b) BM 551003, young adult male; c) RMNH 28073, young male, lectotype of *C. ornatus pletharicus*.

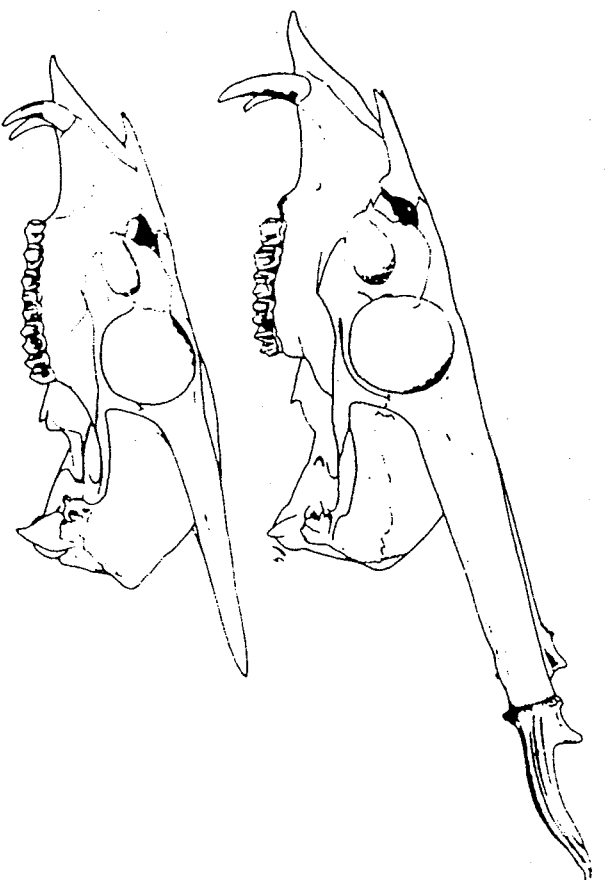


Fig. 1. Skulls of (above) *Munitarius montiae pletharicus*, young adult male (USNM 131501, holotype of *M. montiae*), and (below) *M. pletharicus* sp. nov., adult male (USNM 100000).

males. No frontal tufts. Ear dark grey to black behind, orange at base, white on side.

Shoulder height recorded as 929 and 1043 mm in two males (BM 551005 and 551006; the latter not fully mature despite its larger size).

Skull (figs. 1–3; pl. 1 figs. a–c; pl. 3 figs. a–c) averaging smaller than in sympatric *M. m. pletharicus* (greatest length of adult males 175–201 mm). Flatter, less robust in both sexes, with reduced frontal ridges and, in males, reduced pedicels, pedicels short (65–88 mm), thin (breadth 10–13.5 mm) and bowed, continuing into minute unbranched antlers (length 16–42.5 mm) without any burr in 2b or of 2b specimens, suggesting that antlers are not shed as a rule. Preorbital pit relatively deep, with a well marked rim all round, so that there is a distinct gap between floor of pit and outer surface of jugal.

Differs from *M. maculoides*, especially sympatric *M. m. pletharicus*, in being lighter, brighter and more yellow-orange in general tone; occiput not contrastingly orange, but dark brown, continuing into a dark nuchal stripe; legs not contrastingly dark; tail dark above; underparts more contrastingly pale, but in terrestrial region and throat not pure white; in the flatter, slightly smaller skull, in the form of the preorbital pits and in the much reduced antlers and pedicels. In the available samples of adults, there is no overlap in pedicel thickness, greatest span of antlers or length of antlers from base to tip between the species (Table 1).

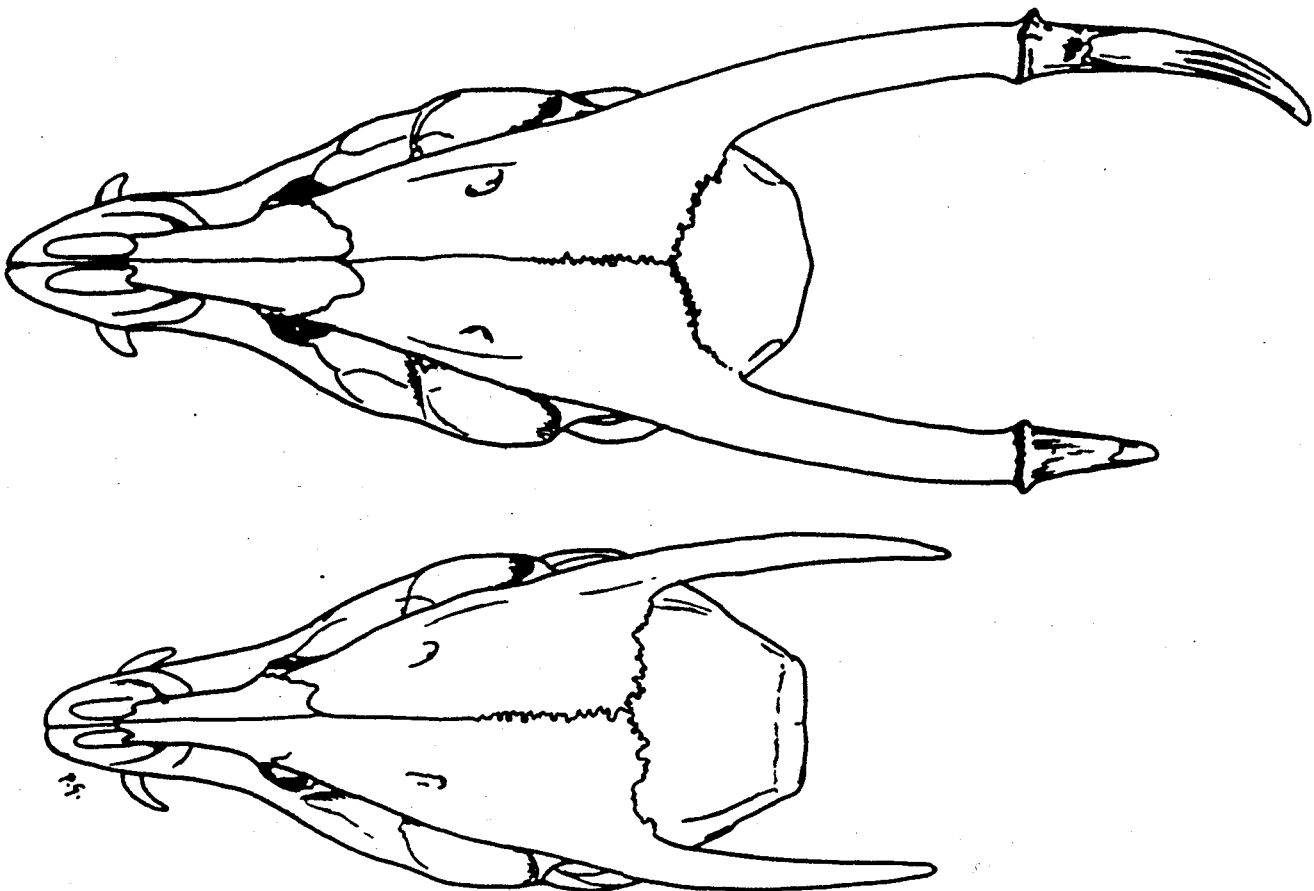


Fig. 2. Skulls of (left) *Muntiacus muntjak pleiharicus*, USNM 151863, and (right) *M. altherodes* sp. nov., USNM 196886.

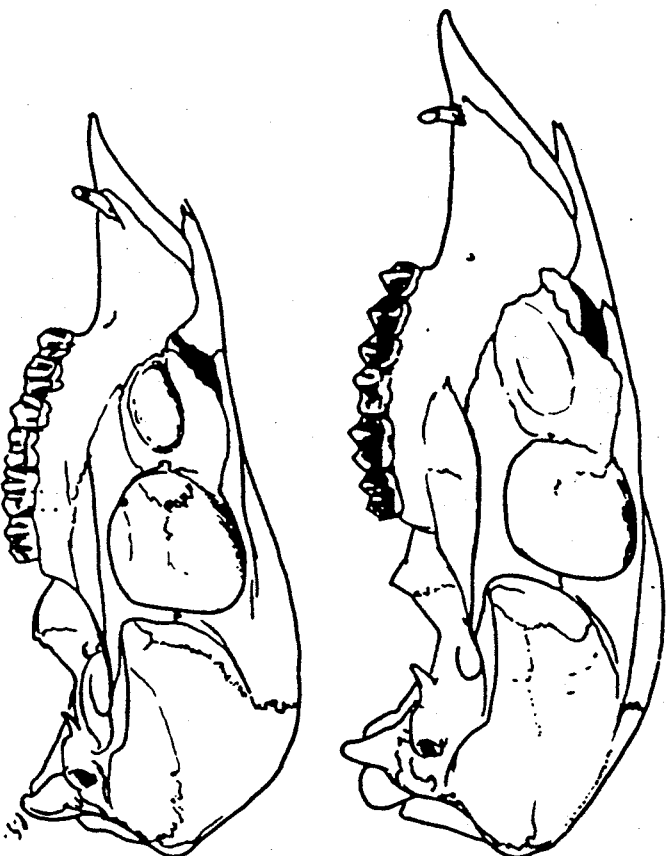


Fig. 3. Skulls of (above) *Muntiacus muntjak pleiharicus*, adult female, USNM 198307, and (below) *M. altherodes* sp. nov., adult female, USNM 197694.

Although skulls of females may not always be easily identified, the striking and discrete differences in colour and colour pattern and in the skulls and antlers of males serve to characterise the two species.

Etymology. — "Like a spike or ear of corn", a reference to the characteristic antler form, from the Greek *ἀθήρα*.

The geographical ranges of the two species overlap widely (fig. 4) and in our samples both species occur at or near the following localities: Pamukang Bay; Kendawangan River; Gunung Dulit; Badang; Paku (Sarebas); Pleihari. As the map shows, only *M. altherodes* seems to occur north of about 4° N in Sarawak or 3° N on the east coast (including the whole of Sabah).

TAXONOMIC POSITION OF *MUNTJACUS ALTHERODES*

The new species differs from all other *Muntiacus* in the absence of the orange occipital patch, the lack of a frontal tuft, the very small antlers and pedicels and the rather well-formed preorbital pit. These characters ally it to the related genus *Elaphodus* and so are most plausibly interpreted as features of primitive retention. If so, *M. altherodes* will be the sister species of all other muntjac, in cladistic terms, and similar — perhaps very similar — to their ancestral species. Other species

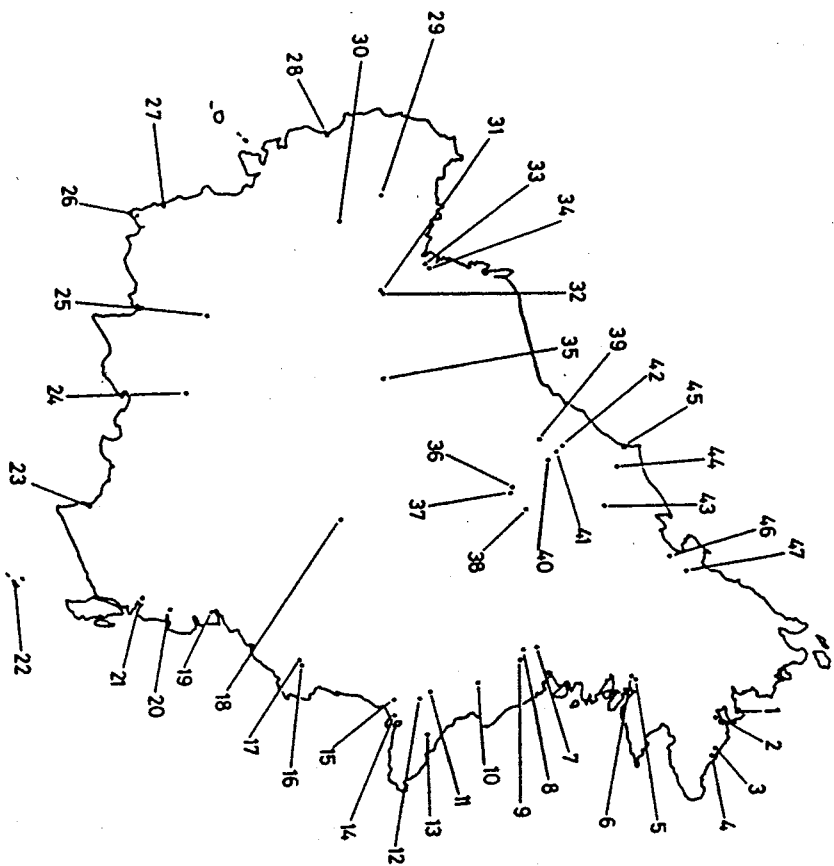


Fig. 4. Map of Borneo showing localities from which muntjac have been recorded: *Muntiacus alfredus* sp. nov. only: 1: near Sandakan; 2: Sapagaya Forest Reserve, Sandakan District; 3: Bukit Keriam, Kinabatangan District; 4: Kinabatangan River; 5: Forest camp 1, Cocoa Research Station, Tawau (type locality of *M. alfredus*); 6: Sungai Tibas camp, Kalabakan, Tawau District; 8: Camp 6, 16 miles north of Mandurau Creek, half a day west of Kaburau on Sungai Kayan (Gyldenstolpe, 1919); 9: Pelaban; 13: Medang; 14: Tanjung Seglu; 15: Sungai Menggane; 16: Batu Panggal near Samarinda; 21: Teluk Klumpang; 24: Parit, Sungai Cempaga, Sampit; 25: Riam, Sungai Kotawaringen; 26: Gunung Talisai; 28: Sonuwang, Landak; 29: Perubuh, Landak; 33: Ulu Paku, Saribas; 36: Sungai Sur, 3rd Division, Sarawak; 37: Sungai Buya, 3rd Division; 41: Bukit Sekiwa, Baram River; 42: Sungai Kejin, 4th Division; 43: Mount Mulu; 45: Miri River; 47: Rayoh (Chasen & Kloss, 1931); *Muntiacus muntjak pletharicus* only: 10: Sungai Birang; 11: Batu Putih; 12: Sungai Karangan; 17: Samarinda; 18: Long Peah, Sungai Mahakam; 19: Sungai Pasir; 22: Pulau Mata Sirit; 30: Sungai Pelandok, Paku, Saribas; 35: Sungai Sibau; 38: Ulu Selio, 4th Division, Sarawak; 39: Sungai Matalum, 3rd Division; 44: Baram River (Marudi?); 46: Spitang; 48: Rejang Valley (exact locus not known; not plotted); 49: Semandung River, west Borneo (not found); 50: Kumru Sompang River (not found). Both species: 7: Badang; 20: Teluk Pamukang (type locality of *Muntiacus rubidus*); 23: Pichari (type locality of *Cervulus pletharicus*); 27: Sungai Kendawangan; 40: Gunung Dulit.

with small antlers and pedicels are *M. fai* of Burma (Grubb, 1977) and *M. crinifrons* of China, which however have large frontal tufts. Superficially similar to each other in their large antlers and other characters are *M. muntjak* and *M. reevesi*, a widespread Chinese species. But these two species differ in their karyotypes (Wurster & Benirschke, 1970) and there is also a karyotypic difference between Indian and southeast Asian forms referred to *M. muntjak* which, in the opinion of White (1978), would result in reduced fecundity of any hybrids between them. It is thus possible that division of the genus into more species may be warranted. On the other hand, the finding that *Muntiacus* (and *Elaphodus*) is a true Cervine (Groves, 1974) suggests that it is at least possible that large antlers are primitive for the genus, and that in those species with small antlers they are secondarily reduced. The frontal tuft and the elongated pedicels common to all muntjac except *M. alfredus* are certainly derived characters, so that the view of the new species as phylogenetically old would still be the most plausible one. The identification of this species adds to the list of Borneo endemic mammals, by Medway's (1977: 8) reckoning, already 20% of 196 species. This is noticeably higher than for the other large islands of Sundaland (Java, 11% of 125 species; Sumatra, 9% of 170 species, according to counts by C.P.G.), and taken together with the presence there of primitive subspecies of such taxa as *Bos javanicus*, *Cervus unicornis* and *Dicotyles sumatrensis*, identifies Borneo as a refuge of the first magnitude.

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