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Notes on the Taxonomy of the Deer (Mammalia, Cervidae) of the Philippines

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With 1 Figure and 3 Tables

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Abstract

Studied the skins and skulls of available specimens of Philippine Deer (*Cervus*, subgenus *Rusa*) in European and American collections, together with the descriptions by PERE HEUDE. Two species can be recognised: *Cervus alfredi* Slater, 1870, from the Visayas group, and *Cervus mariannus* Desmarest, 1822, from Luzon, Mindanao etc.; the latter having subspecies for Luzon, Mindoro, Mindanao lowlands and Mindanao highlands. The evolutionary status of these deer is discussed. *Cervus timorensis* does not occur on the Philippines; there is however an *Axis* on the Calamianes and a *Sika* on the Sulu archipelago.

Introduction

The relationships of the Philippine deer to each other, to the deer of the Marianas and the Bonin Is., and to other rusine deer are still a matter of controversy (DOBROKINA 1971, VAN BEMMEL 1974). As their taxonomy is even now poorly understood, and their nomenclature confused, we here present a critical review of their status together with some tentative conclusions.

Most Philippine deer belong to the *Rusa* group (here assigned to *Cervus* as a subgenus, but regarded as a full genus by some other authors), but *Sikelaphus soloensis* (Heude, 1888) from Jolo in the Sulu archipelago is an ally of *Cervus nippon*, and *Hylaphus calamianensis* (Heude, 1888) (synonym: *Cervus culionensis* (Elliot, 1897) from the Calamianes Is. is a representative of subgenus *Axis* related to *porcinus*, although as recently as 1952 SANBORN followed HOLLISTER (1912, 1913) in placing it mistakenly in *Rusa*.

Material and Techniques

We have examined specimens in the Rijksmuseum van Natuurlijke Historie, Leiden; the British Museum (Natural History), London (BM); the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); and the National Museum of Natural History, Washington (USNM).

Skulls have been assigned to age groups according to the state of eruption of the maxillary dentition. In "adults" M3 has erupted, is in wear, and has closed infundibula. In "subadults" M3 has erupted but the infundibula remain open. "Juveniles" are animals in which M3 at least has not yet erupted.

Conventional skull measurements have been recorded; in addition we have measured pedicle length as the least distance between the orbital rim and the burr; antler length as

the greatest straight length between the burr and the tip of antero-external terminal tine; and antler span as the greatest span of the antlers.

A high proportion of the specimens seen consists of single antlers or frontlets with antlers, and although these provide locality records they can usually not be aged, so they are of limited value taxonomically.

Chronological List of Previous Works

Contributions to the taxonomy of Philippine deer have been made by a number of authorities, and in considering their views and our own, we think it best to list the important contributions chronologically and then to examine the Philippine rusine deer and their relatives island by island, before presenting our taxonomic conclusions.

- 1822: DESMAREST describes *Cervus mariannus* (Guam).
 1827: HAMILTON SMITH describes *Cervus philippinus* (Luzon) as a species of muntjac.
 1876: SCLATER describes *Cervus alfredi* ("Philippines").
 1877: BROOKE describes *Cervus nigricans* ("Philippines") and reviews Philippine deer, recognising the four species mentioned so far though suggesting that *C. mariannus* and *philippinus* are almost certainly conspecific.
 1888: Description by HEUDE of numerous forms, mainly from Luzon, and of two new endemic genera: *Melanaxis* to include *alfredi* and several new species, and *Ussa* to include *mariannus*, *philippinus* and *nigricans* together with numerous new species, including *basilaniensis*.
 1897: ELLIOT describes *Cervus steerii* (Basilan).
 1898: LYDEKKER regards *C. mariannus* and *philippinus* as conspecific and believes *nigricans* to be the prior name for *steerii*.
 1899: HEUDE describes more forms, but suppresses some of his earlier names.
 1900: LYDEKKER describes *Cervus (Rusa) lavistocki* (Philippines?).
 1905: LYDEKKER describes *Cervus (Rusa) unicolor boninensis* (Bonin Is.).
 1912: HOLLISTER provides a checklist of all nominal species.
 1913: HOLLISTER describes *Rusa nigellus* (Mindanao) and enumerates specimens mostly collected by E. A. MEARNS of *Rusa philippinus* (Luzon), *R. barandanus* Heude (Mindoro), *R. francianus* Heude (Mindanao) and *R. basilaniensis* Heude (Basilan), the last being regarded as separate from *R. nigricans* (Basilan), of which *steerii* is given as a synonym.
 1915: LYDEKKER reviews the Cervidae and recognises from the Philippines *Cervus (Rusa) alfredi*, *C. (R.) lavistocki* and *C. (R.) unicolor* with subspecies *philippinus*, *barandanus*, *francianus*, *basilaniensis*, *nigricans* (syn. *steerii*) and *nigellus*, as well as *mariannus* and *boninensis*.
 1920: MOHA reviews rusine deer, recognising two species in the Philippines, a spotted one (*alfredi*) referred to *Axis*, and the unspotted *Rusa equina philippinus* (syn. *nigricans*). *Boninensis* is synonymised with *R. e. equina*.
 1934: TAYLOR reviews the mammals of the Philippines and recognises seven full species of rusine deer (*philippinus*, *alfredi*, *barandanus*, *francianus*, *basilaniensis*, *nigellus* and *nigricans* (syn. *steerii*)).
 1935: POCOCK, surveying the incisiform teeth of deer, separates *Ussa* (includes *nigricans*, *boninensis* and *philippinus*) and *Melanaxis* (for *alfredi*) from *Rusa*.
 1943a: POCOCK regards *philippinus* as a synonym of *mariannus*, with *steerii* a synonym of *basilaniensis*, both forms being this time regarded as subspecies of *Rusa unicolor*.
 1943b: POCOCK recognises *R. nigricans* as a separate species, of which *boninensis* is made a subspecies.

1952: SANBORN describes new material of *alfredi* (Negros) and *francianus* (Mindanao), both listed as species of *Rusa*, and describes *R. nigellus apoensis* as a new subspecies from Mindanao.

1963: HALTENORTH reviews the Artiodactyla and recognises three species of *Cervus* subgenus *Rusa* — *C. unicolor*, with *equina* a subspecies; *C. timorensis*; and *C. mariannus*, with subspecies *mariannus* (syn. *philippinus*); *alfredi*; *barandanus*; *francianus*; *basilaniensis*; and *nigellus*.

1971: DOBROUKA revives Heude's generic name *Ussa* in a subgeneric sense with *Melanaxis* a synonym. He does not give full synonymy but recognises the following species: *R. (Ussa) alfredi* (various islands), *R. (U.) mariannus* with subspecies *mariannus* (syn. *nigricans*) (Luzon, Mariana Is.) and *basilaniensis* (syn. *nigellus*) (Basilan, Mindanao), and *R. (Rusa) timorensis* subspecies *philippinus* (Luzon, Mindanao).

1974: VAN BEMMEL places all rusine deer in a single superspecies yet accepts, with reservation, the interpretation of DOBROUKA.

Deer Populations on the Different Islands (see map, Fig. 1)

1. Mariana islands

Cervus mariannus Desmarest, 1822: this name was based on a specimen collected by QUOY and GAIMARD on Guam. BROOKE (1877) thought it was probably a senior synonym of *philippinus*, and POCOCK (1943 a) considered the two names to

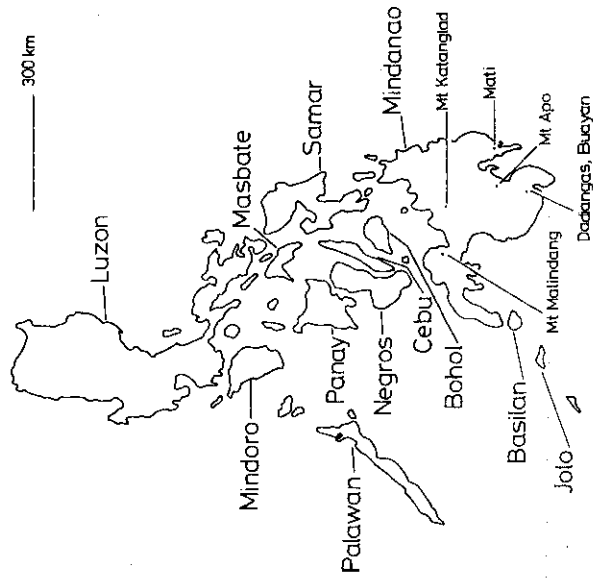


Fig. 1

be definitely synonymous; more recently ДОБРОРУКА (1971) has disagreed with this. HEUDE (1888) considered *mariannus* to be a composite species, for he recognised several of his nominal Luzon species in the series of 43 Marianas specimens he had before him. This, more than anything else, confirms the identity of Luzon and Marianas forms! But HEUDE had not seen the type of *mariannus* so could not identify it typologically with any of his names.

It seems very unlikely that deer are native to the Marianas, but we know of no direct evidence that they were introduced there, nor that Luzon was the source of the population.

2. Caroline islands

Rusine deer are also present on the Caroline Islands at least on Ponape (USNM specimens).

3. Bonin islands (Ogasawara Gunto)

Cervus (Rusa) unicolor boninensis Lydekker, 1905: this form is known from the adult female holotype skull, and the skin and broken skull of a subadult male with apparently malformed antlers. Deer are certainly introduced to these islands, perhaps from the Philippines (Pocock 1943 b), but the matter is complicated and will be discussed in a future paper.

4. Philippines (precise origin unknown)

Cervus tabistocki Lydekker, 1900: this name is based on a menagerie specimen, a mounted skin with abnormal antlers (BM 0.6.8.2), the only one preserved out of a group belonging to the Duke of Bedford (see photograph of living animal in LYDEKKER, 1898). LYDEKKER (1900) said these animals resembled *Cervus (Rusa) timorensis* in general form, relatively thin tail, slight rugosity of the antlers and annulation of the hairs with black and yellow. He says, "no definite information is available with regard to their place of origin, although it is probable that they came from the Philippines". It seems much more likely that they came from some other archipelago, and the name should be regarded as a synonym of *timorensis*, rather than evidence for that species occurring on one of the Philippine group. It is noteworthy, too, that Pocock (1935) placed the species in *Rusa*, not in *Ussa*, on the characters of its incisiform teeth; he saw what was apposed Basilian type skull of *tabistocki* (BM 2.5.3.1) but it cannot now be found.

Cervus nigricans Brooke, 1877: this nominal species — the source of so many headaches in the taxonomy of Philippine *Rusa* — is known with certainty only from the holotype which consists of the skin and skull of a menagerie specimen said to have come from the Philippines. HALTENORTH (1963) lists it as a *nomen nudum* and a synonym of *francianus*, but it is a perfectly valid name as ДОБРОРУКА (1971) has emphasised, and has priority over *francianus* and all HEUDE's other names. It has been associated with dark coloured deer from Luzon (HEUDE 1888), with the Basilian *rusa* (LYDEKKER 1895), and with the smaller of two supposed Basilian species to include *steerii* as a synonym but not *basilianensis* (HOLLISTER, 1913, followed by LYDEKKER, 1915). Pocock (1943 b) provisionally accepted HEUDE's interpretation, but only in part: HEUDE drew attention to two specimens, a male with broken tines and a female, but Pocock noted the female only, as the male cannot be singled out from other Luzon *rusas* illustrated in HEUDE's work. Because of its short skull and the form of the nasals (rather difficult to interpret in the small illustration), as well as HEUDE's statement that it had dark pelage, Pocock ten-

tatively suggested that this female specimen at least might represent a smaller species of *rusa* on Luzon, separate from what he called *Rusa unicolor mariannus*. His chief reason for keeping *nigricans* (including *boninensis*) as a species separate from *Rusa unicolor* was the absence of canines. The lachrymal fossa is large and the nasals are "non-cruciform", characters which he alleged are atypical for Philippine *rusas* yet which are certainly normal for rusine deer from other regions. The nasals are particularly short and narrow in *nigricans* and in this character the skull differs from that of all other rusine deer.

Pocock's concept of *Rusa nigricans* is unsatisfactory, being based on two specimens from a non-native population of unknown derivation (*boninensis*), on a menagerie specimen of unknown origin (type of *nigricans*), and on a drawing from HEUDE. Pocock made no analysis of any other illustration of HEUDE's, so did not suggest whether they could support his two-species theory.

There is a possibility that the skull of *C. nigricans* is distorted as a result of captivity, an effect well documented in other species (see e.g. HOLLISTER 1917, GROVES 1963), and it is worth examining the specimen's diagnostic features in terms of such an assessment. Pocock (1943 a) did not refer to any abnormal characters, though in another paper (Pocock 1942) noted exceptional variation within *Cervus unicolor swinhoei* of Taiwan which presumably is due to the inclusion of both captive and wild shot specimens in the sample. BROOKE (1878) refers to dish-faced skulls with high foreheads in badly nourished deer; the *nigricans* skull shows this feature to some extent and also has a noticeably short, narrow and upturned muzzle, as well as the shortened nasal bones. Other captivity specimens of rusine deer in the BM are even more distorted, though like *nigricans* their ossification appears to be normal. BM 1815.12.8.30 (1427c) labelled "*moluccensis*" (*Cervus timorensis*?) is distorted in a similar way but to a greater extent, having an exceptionally short, upturned muzzle. BM 97.4.3.2 labelled *timorensis* is very short faced too but also has a remarkably broad skull. BM 79.3.20.1, a female *C. alfredi*, is particularly similar in proportions to *nigricans*, but has prominent signs of desiccation, especially in the nasal region; it is much shorter in length than wild-shot specimens from Negros (Tab. 1).

The absence of canines in *nigricans* may also result from captivity. In the female *alfredi* skull, there is no trace of canine or alveolus on one side. The male holotype of the same species had lost its canines, and sealing up of the alveoli was in progress at the time of death. Occasional wild shot specimens may lack canines — for instance deer from Guam and Mindoro. It is evident that too much significance was attached by Pocock to the absence of canines in *nigricans* and *boninensis*.

The character of the nasals and lachrymal vacuities also deserves comment. The nasals broaden proximally in most *rusas* and are broadest where they form the medial margin of the lachrymal vacuities. In most Philippine deer, these vacuities show a tendency to be closed, partly by an ingrowth of the maxilla, and partly by an outgrowth of the nasals. In the unspotted forms, this outgrowth leads to each nasal being bifurcate at its base, one fork entering the lachrymal vacuity and the other suturing with the frontal, together forming a crude cruciform figure (Pocock 1943 a, ДОБРОРУКА 1971). The distinction between cruciform nasals and nasals with unbifurcated bases is not always a clear one, as the nasofrontal suture is often irregular in shape, while the degree to which the vacuities are sealed also varies. This character is much more strongly developed in males than in females, where the vacuities are never fully sealed (see illustrations in HEUDE 1888) and where the nasals are not always cruciform. Once again, we think Pocock (1943 b) attached too much significance to this character, probably because he was comparing the

female *nigricans* skull with male skulls of other Philippine deer and was not aware of potential sexual dimorphism.

The holotype skin of *nigricans* has unfortunately been dismounted, so is not in the best of condition. It is dark brown, very uniform in tone, but darker on occiput, snout, back of neck, a line down the neck and on the tail, and with a faint ochrey wash on the outside of the legs and on the hindquarters. The groin is dirty buffy, the inside of the limbs and axilla more a dull ochrey tone. There is ochraceous speckling all round the eye and preorbital gland and on the occiput. The chin is pale but there are no discernible dark markings round the mouth. The original description and figure (Brooke 1877) gives the impression of a much blacker animal, but LYDEKKER (1915) did not think it differed from a specimen of the Basilan rusa. We conclude in turn that the darker Mindanao deer are not separable in pelage characters from the deer of Basilan, and that (assuming its skull characters are abnormal), *nigricans* should be regarded as the prior name for these deer. Cervus *alfredi* Selater, 1870: this spotted deer was described from a male and female in the London zoo, said to have come from the Philippines, and BROOKE (1877) said they had been sent from Manila. There is no evidence that the spotted rusa occurs on Luzon, and indeed it has never been supposed to do so.

Melanaxis (?) *elegans* Heude, 1888: This name was based on a pair of antlers of unknown origin; in 1899, HEUDE applied it to a male skull which he had earlier identified as *Melanaxis alfredi*. There is no direct evidence, however, that the type of *elegans* was a spotted deer, so synonymy with *alfredi* is conjectural.

Ussa gonzalimus, *U. villemarianus*, *U. crassicornis* Heude, 1888: the type localities for these names are not known. HOLLISTER (1912) followed by LYDEKKER (1915) gives the type locality of *villemarianus* as "San Miguel de Murcia, Tartlac, Luzon", but HEUDE himself mentions no locality in either 1888 or 1899. The origin of *crassicornis* is given as Cebu by HEUDE (1888) followed by HOLLISTER and LYDEKKER, but in 1899 HEUDE admits that this was wholly conjectural.

5. Luzon

Cervus philippinus H. Smith, 1827: the holotype, a "very poorly preserved" young male collected by DUSSUMIER, was seen by BROOKE (1877) at the Paris Museum, but is no longer extant; DE BEAUFORT (1964) states that DUSSUMIER's specimen no longer exists, and lists only the types of *Cervus philippinus* Pucheran, 1855, and a further search by one of us (C.P.G.) in 1973 could not locate it. BROOKE has given a description of the specimen, though the accompanying plate is of another individual (of unknown origin); he thought that *philippinus* should be treated as conspecific with *mariannus*, and this suggestion was adopted by Pocock (1943 a).

DOKOROKA (1971), however, disagrees with this verdict, listing *philippinus* as a subspecies of *Rusa timorensis*. He lists his material of *Rusa marianna* but does not say what material of *R. t. philippina* he has seen; the only specimen mentioned is an animal formerly in Berlin zoo, purchased from Manila. There is thus no certainly identifiable locality involved; from his plate of the living specimen it is quite clear that the latter was indeed a *timorensis* (of one of the smaller, maneless races diagnosed by VAN BEMMEL (1949)), but in view of the fact that our own researches have turned up no specimen of the latter species from the Philippines it is unlikely that the zoo specimen was actually captured in the Philippines.

As for the type of *Cervus philippinus*, BROOKE's description of it as having "one short tine directed inwards" would seem to indicate *equinus*-type antlers, not *timorensis*-type, so that it could really have come from Luzon as has been generally interpreted.

Table 1. Mean \pm one standard deviation of skull and antler measurements (mm) of Philippine deer. Sample size (*n*) is given also where data are based on only one or two measurements, due to broken specimens in the sample

n	C. affinis:		C. m. mariannus		C. m. baraduanus:		C. m. nigricans:		n
	Holotype, adult	Negros, adult	Luzon, subadults	Guam, adult	Guam, subadults	Kota, adult	Ponape, adults	Mindoro, adults	
1	266	137	80	48	48	40	77	81	72
1	264	145	90	40	77	81	103	104	68
1	271.5 \pm	140.4 \pm	91.3 \pm	45.0 \pm	75.0 \pm	85	114.5 \pm	73.0 \pm	63
6	271.5 \pm	140.4 \pm	91.3 \pm	45.0 \pm	75.0 \pm	85	114.5 \pm	73.0 \pm	63
3	260.7 \pm	133.2 \pm	81.50 \pm	42.8 \pm	80.3 \pm	80.7 \pm	110.7 \pm	77.0	83.0
3	14.98	10.32	8.05	6.01	3.06	2.08	2.89	(<i>n</i> = 2)	83.0
3	267.0	139.8 \pm	93.0 \pm	44.3 \pm	82.7 \pm	80.3 \pm	112.5 \pm	73.8 \pm	65.8 \pm
3	267	137.7 \pm	85.8 \pm	45.0 \pm	84.5	80.0 \pm	112.2 \pm	74.5 \pm	67.3
1	279	143.5	90.5	—	79.5	—	116.5	76	58
2	294.0	151.5	103.0	42.5	83.0	78.0	120	79.0	63.5
4	262.0 \pm	132.5 \pm	97.0 \pm	35.1 \pm	57.8 \pm	92.5 \pm	108.3 \pm	67.9	77.3 \pm
4	12.38	9.26	9.11	1.31	7.50	3.42	3.95	1.18	1.85
2	265	143	88.0	43.0	78.8	72.0	102.0	71.5	76.0
2	234.5 \pm	123.8 \pm	76.2 \pm	31.5	73.0 \pm	69.8 \pm	98.0 \pm	66.8 \pm	64.3 \pm
3	5.63	0.29	1.61	(<i>n</i> = 2)	4.04	3.69	5.27	2.02	6.66
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)	(<i>n</i> = 1)
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
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2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
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2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
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2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.5	69.0	71.0	105.5	68.3	52.0
2	235.0	121.0	78.0	38.5	70.5	69.5	101.5	91	58
2	257	136	87.0	42.					

Table 1 (continued)

n	Greatest length	Preorbital length	Nasal length	Greatest Maxillary breadth	Palate breadth	Rostral Braincase width	Orbital breadth	Pedicle length	Antler length	Antler span
1	209	101.5	59	30	62	94	62	—	204	193
3	215.7 ±	110.8 ±	71.2 ±	29.3 ±	70.01	64.5 ±	84.8 ±	61.3 ±	177.0	191.5
1	—	10.12	5.69	1.04	2.93	2.18	3.89	1.15	(n = 2)	(n = 2)
1	—	104	67	34	64	63	91	64	67	113
1	—	—	—	34	62	80	108	—	—	—
2	242.5	130.5	80.3	34.0	72.8	69.0	89.5	62.8	—	—
1	224	114.5	—	—	67	79	99	66	—	—
1	238	124.5	76.5	36.5	79	71.5	95	66.5	—	—
1	—	133	84	36	82	80	105	—	—	—
7	—	132.1 ±	85.2 ±	33.4 ±	79.8 ±	74.4 ±	96.4 ±	66.4 ±	—	—
1	253	139	—	43	2.00	1.13	1.89	1.56	73	—
1	226	118	64	29	76	77	96	—	—	—
1	245	130	79	38	73	76.5	97	64	—	—

Table 1 (continued)

n	Greatest length	Preorbital length	Nasal length	Greatest Maxillary breadth	Palate breadth	Rostral Braincase width	Orbital breadth	Pedicle length	Antler length	Antler span
1	236	125.5	84.5	41	68	67	89	65	—	—
1	211.5	113	68	31	69.5	64.5	83	64	—	—
1	227.5	120.5	76.5	35	62	68	91.5	66	—	—
1	202	104	—	23	65	64	86	60	—	—
1	213	110	73	25	71	69	82	59	—	—
1	247	128	77	40	—	79	107	—	—	—

(b) Females

Ussa spp. Heude, 1888 and 1899: numerous new "species" were described by Heude from Luzon. They are listed in the taxonomic section (see below).

In the 1899 paper, the 1888 list was revised somewhat: some names being reduced to synonymy (explicitly or by implication), some new ones being created using specimens previously assigned to other nominal species, and referring several illustrations from his 1888 paper to different nominal species. Under these circumstances localities and names are now rather difficult to correlate satisfactorily!

Heude never saw the type of *Cervus philippinus*, so he was unable to identify it typologically with any of his nominal species. From his illustrations, the estimated skull length (occipital crest to premaxillary tips) of most of his Luzon specimens lies between 240 and 260 mm, a range of 20 mm which, as it includes animals of different ages, is quite comparable with ranges available from specimens we have examined (Tab. 1). Where Heude frequently uses "skull length" the posterior measuring point is the back edge of the foramen magnum, giving a measurement more comparable (probably, within 2-3 mm either way) to condylobasal length than to "greatest skull length". His only "skull length" given for a Philippine deer is 27 cm for *U. michaelinus*; our estimate from his illustration is 260 mm, suggesting that there are limits to the otherwise admirable precision of the draughting. The estimated measurements give a range below that for other Luzon deer (Tab. 1); another reason for being duly cautious about using them for other than internal comparative purposes.

Four of Heude's species are somewhat outside this range, judging by the illustrations, with a skull length estimated at 225-235 mm; they are thus smaller than the others in Heude's work, and much smaller than those listed in Tab. 1. The four in question are: male *U. ambrosianus*, female *U. cf. nigricans*, male *U. garcianus* and male *U. rosarianus*. To what extent these figures might be due to immaturity is not apparent, but all three of these "races" for which toothrow measurements are given by Heude (Tab. 2) are given very small toothrow lengths.

The skulls of Luzon rusa are broader and less prognathous than in *equinus*-group deer from Indo-China likewise illustrated in Heude's work (1888). The skulls of *U. spatharius*, *U. ambrosianus* and most particularly *U. corteanus* are especially short-faced.

The lachrymal fossa appears to be of moderate size in most of the illustrations, and much smaller than in the *equinus* illustrations. It is almost fully sealed in *U. spatharius* and *U. ambrosianus* and reduced to a slit in *U. rosarianus* and *U. michaelinus*, with the anterior margin everted. Both the latter have very large antlers. The nasals are more or less cruciform, typical for Philippine rusa, in most specimens.

Antler length from burr to tip of outer terminal tine is estimated as from 240-430 mm with two larger (*U. michaelinus* and *U. baryceros*) as 470 and 480 mm. When the drawings of antlers in Heude's works are copied onto tracing paper in order of greatest straight length, they form a beautifully graded series. In the smaller antlers, the brow tine is relatively smaller and the inner terminal one relatively shorter. The larger antlers are more rugose and stouter with a relatively larger brow tine and a longer inner terminal tine. Both the terminal tines bend inward to a greater extent. The antlers of *U. spatharius* are rather smooth and particularly small, relative to the size of the skull, while those of *U. ambrosianus* are slender for their length, with very weak terminal tines.

Greatest span of antlers is estimated at 190-350 mm with four specimens (*dailardianus*, *rosarianus*, *michaelinus*, *baryceros*) at 410-495 mm.

Table 2. Upper toothrow lengths of Philippine deer, from Heude (1888) (from Luzon, unless stated otherwise)

'Species'	Toothrow length (mm)
<i>ambrosianus</i>	75
<i>barandanus</i> (Mindoro)	84
<i>brachyceros</i>	90
<i>chrysostrichos</i>	80
<i>corteanus</i>	88
<i>crassicornis</i>	98
<i>dailardianus</i>	90
<i>elorzanus</i>	90
<i>francianus</i> (Mindanao)	78
<i>garcianus</i>	80
<i>gonzalinus</i> (no locality)	90
<i>gorrichanus</i>	81
<i>guidoteanus</i>	94
<i>hipolitianus</i>	85
<i>longicusplis</i>	98
<i>macarianus</i>	85
<i>maraisianus</i>	92
<i>marzaminus</i>	85
<i>microdontus</i>	77
<i>nubianus</i>	85
<i>ramosianus</i>	90
<i>rosarianus</i>	86
<i>rubiginosa</i>	82
<i>spatharius</i>	90
<i>telesforianus</i>	88
<i>tuasoninus</i>	95
<i>perzosanus</i>	98

Heude gives measurements of maxillary toothrow length, with a range of 75-98 mm, a span comparable to that of 90-109 mm for the Bornean subspecies, *C. u. brookeri* (USNM specimens), but exceptionally wide (even taking mesial drift with age into account) when compared with the range for specimens measured by ourselves from any one of five different islands in the Philippines, the widest being 62 to 80 mm for all Mindoro deer. Heude's toothrow measurements also seem rather large compared to our estimates, from his scaled drawings, of skull measurements. We do not know, of course, how Heude took his measurements - whether for instance he measured the toothrow at crown or alveolus.

Measurements estimated from the drawings are perhaps easier to appreciate. The variation in antlers is precisely what one would expect in a natural population, the differences in their size and changes of shape with size indicating antlers grown by animals of different ages. Specimens with large antlers are mature animals with measurements at one extreme of the range for their age group; *michaelinus* and *baryceros*, with their everted and partly sealed lachrymal fossae, are exceptionally well-grown individuals. Small animals, such as *U. ambrosianus* (with closed lachrymal fossae, thin antlers, short face) and *U. spatharius* (closed lachrymal fossae, very short antlers, short face) may represent aged specimens, dimi-

nished in size as sometimes occurs in ungulates (Thomson's Gazelle (Brooks 1965); Black Rhinoceros (GODDARD 1970); Burchell's Zebra (CROVES, unpub.)) and with "degenerate" antlers. It might be remembered also that HEUDE himself, and doubtless some of his suppliers (mostly Catholic missionaries), liked to keep deer in captivity or semi-captivity and use them as "specimens" at death; and this could lead to dwarfing. It is possible, of course, that these and perhaps some of the other smaller specimens of HEUDE's really do represent a distinct population, perhaps regionally separated on Luzon: HEUDE's locality records are mostly the names of Luzon provinces and they may merely reflect the addresses of his correspondents. But until Luzon deer from precisely known localities are examined, it will not be possible to say whether they represent a uniform population or a geographically varying one. The fact that HEUDE did not recognise major divisions among his wealth of Luzon species, though well aware of the differences between the *equinus* and *timorensis* groups and the Philippine deer and between "*Melanaxis*" and "*Ussa*" within the latter assemblage, does suggest that discretely different forms are not discernable. Moreover the available measurements are not clearly bimodal. We can, it seems, be reasonably sure that a dwarf form, analogous to *nigellus* and *apoensis* on Mindanao, has not yet been located on Luzon. And the evidence for sympatric species is even more inadequate (see under Basian also); certainly we cannot accept that *timorensis* deer are present (contra DONOROKA 1971) for all the 30 adult male skulls from Luzon illustrated by HEUDE are of the *Ussa* type. For the present, therefore, we adopt the view that there is but one form of deer on Luzon, for which the prior name, on the evidence listed above, is *marianus*.

6. Mindoro

Ussa barandanus Heude, 1888: the specimen of this form illustrated by HEUDE (1888) has antlers whose length, span and shape fall within the modal values for his Luzon series.

7. Mindanao

Ussa francianus Heude, 1888: this name is applicable to the larger deer on the island (see below, taxonomic section).

Rusa nigellus Hollister, 1913 (Mt Malindang) and *Rusa nigellus apoensis* Sanborn, 1952 (Mt Apo): the measurements of these two montane forms appear to be well outside the ranges of all other Philippine deer (Tab. 1).

HOLLISTER (1913) records *francianus*, as well as *nigellus*, from Mt Malindang, but the evidence for the former is a shed antler only, which presumably cannot be aged and, therefore, is hardly an adequate indication of sympatry. WHITEHEAD'S (1972) report of both species at low altitudes on Mt. Apo would seem to be based on a misreading of SANBORN. We will return to this question in a later section.

8. Basilan

Melanaxis (?) *basilanensis* Heude, 1888: by placing this species in *Melanaxis*, albeit provisionally, HEUDE implied it was a spotted deer, though this is not in fact the case.

Cervus steerii Elliot, 1897: this putative species has been the subject of some controversy, not unconnected with the rather sterile *nigrificans* controversy (see above). LYDEKKER (1898) identified *steerii* with other specimens from Basilan in the British Museum, and quoted STEERE to the effect that only one species of deer

occurs on the island. As this was a relatively small form (not however as small as ELLIOT'S type specimen, a subadult, would at first sight suggest), he assumed that *nigrificans* was the prior name. HOLLISTER (1913) supposed that HEUDE'S *basilanensis* represented a larger species present on Basilan, and referred to the smaller one as *nigrificans* (synonym *steerii*). LYDEKKER (1915) then compromised, and recognised two subspecies of a single species on Basilan, *nigrificans* (synonym *steerii*) and *basilanensis*, and it remained for Pocock (1943 a) to emphasise that the type of *steerii* is not in fact adult, so that the name does not indicate a dwarf form, and is certainly to be associated with the British Museum specimens studied by LYDEKKER; and that there is no reason whatever to associate it with *nigrificans*. He also drew attention once again to STEERE'S observation. It is *nigrificans*, which cannot for any reason be ubicated to Basilan, which should be regarded as separate.

9. Cebu

Ussa cinereus Heude, 1899: this name is based on a juvenile, whose adult colouration was presumably unknown to HEUDE. ELERA (1895) records *Rusa alfredi* from the island. The name *Ussa crassicornis* cannot be connected with Cebu (HEUDE, loc. cit.).

10. Masbate

Melanaxis masbatensis, *M. breviceps*, both of HEUDE, 1888: both names are based on females of the spotted type of *rusa*, so may be provisionally regarded as synonyms of *alfredi*.

11. Guimaras

HEUDE (1888) recorded a male skull of "*Melanaxis alfredi*" from this island, but in 1899 referred the specimen to his *Melanaxis elegans* of which the type locality, pelage and cranial characters are unknown. SANCHEZ (1898) records *alfredi* from Guimaras. According to a correspondent of WHITEHEAD (1972), deer are now extinct both here and on Cebu.

12. Negros

SANBORN (1952) reports a small series of *Rusa alfredi* from Negros.

13. Leyte, Samar

LYDEKKER (1898) records *alfredi* from Leyte and Samar, based on a note of MEYER (1879) whose acquaintance had obtained a specimen on (one of) these islands. This was in fact the first published record of the habitat of *alfredi*-like deer.

14. Panay

ELERA (1895) records *alfredi* from here.

15. Calamianes Is.

Hyelaphus calamianensis Heude, 1888; *Cervus culionensis* Elliot, 1897: this deer has been obtained from the Calamianes group (Culion and Busuanga) on at least four separate occasions (HEUDE 1888, ELLIOT 1897, LYDEKKER 1915, SANBORN 1952). It is a representative of the subgenus *Axis* and is often associated with the hog deer (*Cervus porcinus*), the Bawean deer (*C. kuhlii*) and the extinct *C. oppennoorthi*

of Java in another nominal subgenus, *Hyelaphus*, apart from *C. axis*, the genotype of *Axis*. Extinct deer from Palawan apparently belong to *Axis sensu lato* (Fox 1970). From the distribution of fossil and recent forms, it is possible to view *C. calamianensis* as a relict. But it is also possible that *C. kuhlii* and *C. calamianensis* are derivatives of *C. porcinus*, introduced by human agency from the mainland. There has certainly been widespread artificial dispersal of pigs and deer, as well as some other mammals, in tropical Asia.

HOOGSTRAAL (1951, 79) strongly suggests that the smaller Philippine islands, such as the Calamianes, were modified more intensely by human settlers than the larger. Clearance and repeated burning in the Calamianes encouraged the development of grasslands with dense deer populations and HOOGSTRAAL thought the deer might have been introduced, perhaps from Palawan, where they later became extinct. As Palawan and the Calamianes are faunistically and geomorphologically part of the Sunda shelf, *Axis* could have colonised them from Borneo, though *Axis* is not known from there as a fossil.

Only a critical review of *Axis* will resolve these uncertainties concerning its history and taxonomy.

16. Sulu Is.

Sikilaphus soloensis Heude, 1888: this is a sika (*Cervus nippon*), not a rusa nor an *Axis*; it is described from Jolo. Its presence may be why Sanchez (1900), records *alfredi*, with a query, on that island — both are spotted deer. Presumably it is introduced, but its taxonomic affiliation needs further study. We know of no evidence for ruses occurring on the archipelago, nor of deer of any kind elsewhere apart from Jolo, but the islands are very poorly known faunistically.

Apart from the specimen illustrated by Heude, there is a skull with fully developed antlers in the American Museum of Natural History. Comparisons with Chinese or Japanese sika have not been made, due to the paucity of material in Western Museums. There is an interesting possibility that *Sikilaphus soloensis* is preoccupied by *Cervus pseudaxis* Eydoux and Souleyet, 1841–1852, a name based on a single stag which its describers obtained in Java. DELACOUR (1931) has identified *pseudaxis* with the sika of north Vietnam (*Sika dugenianus* Heude, 1884 — see GLOVER 1956) but the holotype could equally well have come from Jolo. As early as 1852, GRAY mentions a view that *C. pseudaxis* may have come from the Sulu Is, but he was not aware on what evidence this opinion was based. A final decision on the validity of names assignable to sika cannot be made at the moment.

17. Other islands

Catanduanes, Marinduque, Tablas, Sibuyan, Bohol and many smaller islands are not known to harbour deer of any kind, though some of them may well do so. As stated above, Palawan appears today to have no deer although quite well known faunistically.

Affinities among rusine deer

Following VAN BEMMEL (1974) and taking account of our own studies, five sub-species groups of rusine deer can be recognised:

1. *alfredi* group.
2. *martianus* group.
3. *equinus* group: Bangladesh (?), India (Assam), Burma, Thailand, Cambodia, Laos, Vietnam, S. China, Taiwan, Malaya, Indonesia (Sumatra, Borneo and various

smaller islands). Antlers relatively much shorter than in the next group, with beam continued into antero-external terminal tine and with the postero-internal tine distinctly shorter and more or less at right angles to the outer one.

4. *unicolor* group: Bangladesh (?), India (except Assam), Ceylon, Nepal, Sikkim. Antlers relatively much larger, with terminal tines subequal or with the postero-internal one the longer. The latter tine bends towards the antero-external one (which continues the beam, as above), so that the angle between them is much less than in *equinus*.

5. *timorensis* group: Java and surrounding islets, Bali and islands to the east, into most (probably all) of which it has been introduced artificially; other introductions have been made to Mauritius, New Guinea and New Caledonia. Antlers fairly large, with the beam continued into the postero-internal tine which is consistently much the longer and stands at an acute angle to the antero-external one. In development the antero-external tine appears as a snag on the spike; in all other rusa, it is the postero-internal tine which appears as a branch of the spike. *Timorensis* also differs from other ruses in the form of the lachrymal vacuity, which extends further towards the orbit and has the lachrymal borders on each side bowed out or converging anteriorly rather than diverging. Other distinctive features of *timorensis* are outlined by VAN BEMMEL (1949).

We should also recognise that the "rucervine" deer (*C. dipaucefi*, *schoenburgki* and *eldi*) are very close to the rusine group and could probably, following FLEKOV (1952), be placed in the same subgenus.

In the form of the antlers, the Philippine deer are most closely related to the *equinus* group, but they differ from this and the *unicolor* group in the following respects:

1. Small size (outside the range of variation of the other groups) and more compact and less rangy build — the 'crouching agouti build' of BROOKE, 1876. This is probably an allometric difference, as there is a similar variation in proportions in *Axis*.
 2. Very short antlers.
 3. Naso-lachrymal vacuity relatively short and tends to be closed up by expansions of nasals and maxillae.
 4. Greater frequency of hair stream reversal on the neck or withers.
 5. Greater contrast between the relatively broad central incisors and narrow lateral incisiform teeth (POCOCK 1935). In this feature the Philippine deer resemble *Cervus (Axis) porcinus* and its relatives. In a later paper, POCOCK (1943 b) was inclined to discount this distinction, on the basis of age variability in *C. unicolor*, but a difference does remain, and the relative enlargement of the lateral incisiform teeth is a progressive tendency discernible in many lineages of ruminants. Again, it has an allometric basis, related perhaps to a need to enlarge the cropping battery in larger, grazing deer.
 6. The tail is relatively short and short haired, differing alike from the thick tufted bush of the *unicolor* and *equinus* groups and the smaller, crested tail of *timorensis*.
- The unspotted Philippine ruses differ further from the spotted Philippine deer (*alfredi*) as well as the *equinus* group in:
7. The tendency for the nasal bones to be cruciform.
 8. The broad, short-faced skull — another allometric effect.
- The *alfredi* group differs from all other ruses in:
7. The remarkably fine and dense pelage.
 8. The relative narrowness of the skull in relation to its length.

9. The spotted coat. VAN BEMMEL (1949) has drawn attention to the presence of spots in some juvenile rusine deer, where the pattern is very similar to that of adult *alfredi*.

Finally, *C. alfredi* differs from the *marianus* group in the tendency for the basals to have a blunt suture with the frontals. They are not cruciform, even though the lachrymal vacuity tends to be sealed.

We regard characters 1, 2, 5 and 6 (shared by *marianus* and *alfredi*) and 7 and 9 (unique to *alfredi*) as primitive characters, for they are features shared also with certain non-rusine deer.

With regard to the phylogenetic relationships among rusine deer, insofar as they can be determined by phenetics, there can be little doubt that the *timorensis* group is very distinct. We feel that if Pocock, who split off *Ussa* from *Rusa*, had had wild-shot material of this species, he would have placed it too in a new genus. We are not in a position to assess the validity of deer genera and subgenera at this stage, so we will not consider the taxonomic rank of *Cervus timorensis* further. We cannot, however justify the subgenera *Ussa* or *Melanaxis*, notwithstanding that *alfredi* is unique in its pelage characters and (after *timorensis* perhaps?) is the most distinct *rusa*: we do believe however that it, like *timorensis*, is entitled to full specific status. The recognition of the *marianus* group as a full species is less certain, for differences from the *equinus* group are mostly size-related, and the subspecies *brookei* of Borneo approaches the *marianus* group in size and in the reduction of the lachrymal vacuities, which penetrate the maxilla to a lesser extent than in others of the *equinus* group. We prefer to recognise *marianus* as a separate species simply because its measurements do not overlap with those of the *equinus* group, and because it shares certain features with *alfredi*, implying an early separation from the *unicolor/equinus* stock. We appreciate that this is a decision based strictly on phenetics, but where there is no zone of contact between distinctive allopatric populations it is perhaps best to be conservative about species limits if only to avoid the cumbersome use of the term 'subspecies group' when referring to the entities involved. A further point is that universally recognised species in other genera of deer — e.g. *Muntiacus* — are probably as divergent as the *marianus* and *equinus* groups.

It would be convenient to recognise *equinus* as a full species also, following VAN BEMMEL (1949), but the larger members of the group are extremely similar cranially to the *unicolor* group, and though we do not know how the groups interact where they meet in northeast India, it does not seem very likely that they could be reproductively isolated. *C. unicolor* is the prior name for the species.

We thus recognise four species of ruses — *Cervus alfredi*, *C. marianus*, *C. unicolor* and *C. timorensis*.

Historical biogeography of rusine deer

The absence of rusine deer from Palawan and the Calamianes suggests perhaps that they did not enter the Philippines through these islands but through the Sulu archipelago. As the Sulu islands are virtually unknown faunistically, it is not profitable to discuss the relative merits of these hypotheses any further.

There was evidently a separation of spotted and non-spotted stocks of ruses on the Philippines and this may have been the result of two invasions. Preliminary studies (CROVES, in prep.) indicate that Negros is much more different faunistically from Luzon and Mindanao than these two are from each other. The rather poor data on the other islands suggest that Panay, Leyte etc. belong with Negros in this respect and this is in accord with bathymetric data. The islands to which un-

spotted ruses are now confined were probably all connected in the Pleistocene (see IXGER 1954) while those on which spotted ruses are positively known to occur, through the presence of specimens, all lay outside this system. However Leyte and Samar, on which *C. alfredi* may occur or have occurred, were involved in the union between Luzon and Mindanao and hence should have unspotted deer. This biogeographical uncertainty has yet to be resolved.

The most parsimonious hypothesis concerning the speciation and dispersal of rusine deer both inside and outside the Philippines would start with a southeast Asian — perhaps Sundaland — species from which a peripheral population diverged to produce *C. timorensis*. The residual population later colonised the Philippines twice, at early and later stages in its diversification. Through further evolutionary change it then developed into a more progressive form (the *equinus* group) which however failed to provide a third colonisation of the Philippines but which dispersed northward and westward to give rise to the *unicolor* group. *C. marianus* and more especially *C. alfredi* may hence have relictuall distributions.

Taxonomy of Philippine rusine deer

Cervus alfredi

Cervus alfredi Slater, 1870. 'Manilla.'

Melanaxis masbatenis, M. breviceps Heude, 1888. Masbate.

This is one of the rarest deer, only 11 museum specimens being reliably recorded. These are 1. the male holotype skull, skin and skeleton; a female skull and mounted skin; and their offspring, in the British Museum, London. The last named specimen can not now be found. 2. HEUDE'S (1888) two female specimens from Masbate, and a male from Guimaras, presumably still in Shanghai; 3. SANBORN'S (1952) two males and three females from Negros, in the Field Museum.

In addition the Duke of Bedford imported a pair in 1904 (HASTINGS 1949) and MOHR (1920) described living specimens in the Berlin zoo.

The male holotype is very dark, almost blackish brown, speckled with ochre subterminal hair bands, which gradually disappear on the lower flanks and neck. The belly, groin, axilla, inside of the limbs, chin and underside of the lower jaw are a sharply contrasting velvety buffy. There is a dark dorsal band bordered with faint dull ochre spots. Below this, on the flanks, the spots are bigger and more scattered. The tail is very dark brown above, buffy below. The legs are noticeably paler than the body below hock and carpus, with a vague darkening down the middle of the shanks. The neck colour grades into the paler tones of the head, where the occiput is dark ochery with dark bases to the thickly matted hairs. The tone is paler, more buffy above the eyes. The rest of the head is paler brown, the hairs dark at the base and with fine dark tips. Black hair surrounds the preorbital glands: there are dark labial and muzzle patches; and the ears are black behind. The tail is short and the whole pelage is thick and very soft. The female BM specimen is similar; the five specimens from Negros are somewhat redder.

The pelage is very fine and remarkably dense and soft in all specimens examined, as already noted by LYBECKER (1915) and Pocock (1935) — quite different from that of all other ruses or, for that matter, all other Old World deer. DONORUKA (1971) considers the long reversed tract of nuchal hair to be a species character, but the adult Negros male has the hair reversed for only 15 cm, and the reversal tract is equally long in several Mindanao deer.

The skull of *alfredi* is narrow compared with those of other Philippine ruses, with biorbital breadth 0.382 and 0.390 of greatest length in two adult males, 0.365

and 0.373 in two adult females. The holotype was in captivity for a long time, and its skull and skeleton are very light, presumably weakly calcified. The nasals are relatively short and broad and the muzzle is also a little short, but in spite of these presumed captivity effects the specimen is very similar in proportions to the adult male Negros skull (SANBORN 1953) and the skull figured by HEUDE (1888). The nasals in *alfredi* do not bifurcate basally and tend to have a broad blunt suture with the frontals, but the lachrymal vacuities nevertheless tend to be sealed.

MOHR (1920) referred *alfredi* to *Axis*, but apart from the spots there is no special resemblance to this subgenus. *C. alfredi*, like other *rusas*, and unlike *Axis*, is said to lack the interdental glands (LYDEKKER 1915), although this needs to be substantiated. The skull proportions are typically *rusine*, and so are the rugose and relatively stout antlers.

We cannot include *Melanaxis elegans* Heude, 1888, in the synonymy of *alfredi* for there is no evidence that it was a spotted deer. Localities: Leyte and/or Samar?; Cebu?; Guimaras; Masbate; Negros: Bugbugtongan and Naliong, Tolong; Bais, Makaba — FMNH.

Cervus mariannus

Cervus mariannus mariannus

- Cervus mariannus* Desmarest, 1822. Guam.
Cervus philippinus H. Smith, 1827. Philippine Is.
Ussa gonzalinus, *U. villemierianus*, *U. crassicornis* Heude, 1888. Philippine Is.
Ussa gorrichianus, *U. tuasoninus*, *U. guidoteanus*, *U. roxasianus*, *U. longicuspis*, *U. microdonus*, *U. telesforianus*, *U. brachyceros* Heude, 1888. Batangas province, Luzon.
Ussa hippolitianus, *U. chrysostrichos* Heude, 1888. Batangas and La Laguna provinces, Luzon.
Ussa nubianus, *U. spatharius* Heude 1888, La Laguna province, Luzon.
Ussa ramosianus, *U. ambrosianus*, *U. macarianus*, *U. garcianus*, *U. rosarianus*, *U. verzoisianus* Heude, 1888. Nueva Ecija province, Luzon.
Ussa rubiginosa Heude, 1888. Bataan and Nueva Ecija provinces, Luzon.
Ussa elorzanus Heude, 1888. Bataan provinces, Luzon.
Ussa cf. nigricans, *U. maraisianus*, *U. dialliardianus* Heude, 1888. Jala Jala forest, Luzon.
Ussa corteanus Heude, 1888. Mariveles, North of Manila Bay, Luzon.
Ussa guevaranus Heude, 1888. Mariguina, Luzon.
Ussa marzatinus Heude, 1888. Infanta, Luzon (see Heude 1899).
Ussa baryceros Heude, 1899. Batangas and La Laguna provinces, Luzon.
Ussa athencensis Heude, 1899. La Laguna province, Luzon.
Ussa michaelinus, *U. vidalinus* Heude, 1899. S. Miguel de Murcia, Tarlac, Luzon.
Melanaxis elegans Heude, 1888. Philippine Is.

We have attached all names based on Luzon deer and most names based on Philippine deer, but without indication of precise locality of origin, to *mariannus*, as discussed in an earlier section.

Only a few skulls of Luzon deer were available to us. They include the flattest and broadest of any Philippine skulls we have seen (see DOBROUKA 1971, Pl. 1), but not all specimens are like this. Skull breadth in adult and subadult males is between 0.399 and 0.462 of greatest length ($n = 7$; see Tab. 1).

Two male and a female skull from Ponape in the Caroline Is. resemble the Luzon deer (Tab. 1) but are larger than any other *C. mariannus*. The males have very stout and rugose antlers, the rugosities developing in places into incipient snags.

Skull breadth is 0.385–0.433 of greatest length in the male skulls, and they fall outside the range of variation of most length measurements for Luzon stags.

We have also seen a series of mostly fragmentary skulls from Guam in the Marianas (Tab. 1). None are as broad as the extremes in the Luzon series — skull breadth is 0.412–0.442 of greatest length in three male skulls — but they have no other distinctive features. A male skull from Rota, also in the Marianas, is slightly larger with heavy rugose antlers like those from Ponape; its skull breadth, 0.417 of greatest length, falls within the range for Guam.

Guam deer in the San Diego Zoo are deep brown with a blackish tinge on the back, paler on the cheeks, slightly paler on the underside, and with a red-ochre wash on the haunches. The tail is white beneath, as are the inner surfaces of the ears; groin and axillae are a mere paler shade of the body colour. Forehead and midface are hardly darker than general body tone, but the muzzle is dark; there is an ochre speckling round eyes and on cheeks, especially in males, and also on antler pedicels. Legs are paler than body, especially on the lower portions. Fawns are lighter than adults, and unspotted (SHERIDAN 1967, 6; DOLAN 1971, 10). These living deer were seen by one of us (C.P.G.) in 1968, but we have seen no museum skins.

Nomenclatural separation of Luzon and Guam deer does not appear to be justified. The deer of the Caroline Is could in theory be taxonomically separated, but we do not think this should be done: not only are the external characters unknown, but they do not represent an aboriginal population and it would be meaningless to separate them nomenclaturally from the putative ancestor *C. m. mariannus*.

Localities: Luzon, Cagayan Province: Abulug; Aparri; Baggao — AMNH; Sorsogon Province: Casiguran — AMNH; Ilocos sur Province — USNM; Sinit — AMNH; Batangas Province: Calatagan — FMNH; Isabela Province: Sierra Madre Mtns — AMNH; Abra Province — USNM; Benguet — AMNH; Mariveles Mtns — USNM. Heude's localities are listed in the synonymy. Marianna Is: Guam — USNM; Rota — USNM; Caroline Is: Ponape — USNM.

Cervus mariannus barandanus

Ussa barandanus Heude, 1888. Mindoro.

Skulls from Mindoro (Tab. 1) are on average narrower than those from Luzon, skull breadth being 0.390–0.425 of greatest length in four males, but the difference is not taxonomically significant. In braincase width, nasal breadth and toothrow length (and bimastoid width) however, the Mindoro deer are significantly smaller, while in palate width they are larger. Sea level fluctuations in the Pleistocene may have brought Luzon and Mindoro in contact, so that gene flow between the populations could have occurred quite recently (see below under the discussion of Mindanao and Basilan), and it may seem a little anomalous to separate *barandanus* from *mariannus* when the unnamed Caroline deer are in some ways even more distinct. Nevertheless, the Mindoro deer are believed to be an aboriginal population and they are metrically distinct on the basis of a rather small sample. On these two counts, they are entitled to retain subspecific identity. The external characters of *barandanus* are still unknown.

Localities: Mindoro — USNM; Municipal — AMNH; Calapan — TAYLOR, 1934.

Cervus mariannus nigricans

Cervus nigricans Brooke, 1876. Philippines.

Ussa francianus Heude, 1888. Mati, Mindanao.

Melanaxis basilanensis Heude, 1888. Basilan.

Cervus steerii Elliot, 1897. Basilan.

could form the basis of a separate subspecies on the evidence of their pale colouration but others are quite close to topotypical *francianus*; all tend to be smaller than typical "francianus", but do not differ cranially from "basilaniensis". The very local differences in pelage colour and coarseness in the Buayan deer are peculiar; coupled with the possibility that their grassland habitat is not an edaphic or climatic climax but the result of human interference, this suggests that they may represent a population introduced, presumably from elsewhere in the Philippines, interbreeding with native deer.

3. "*Basilaniensis*" appears at first sight to be smaller than "*francianus*" but the evidence for this proves to be inadequate when animals of the same age class are compared (Tab. 3) and is complicated by the possibility of regional size variation in "*francianus*". The pelage is not distinctive. One might suppose that the major divergence among these deer would be between the populations of the two islands, Basilan and Mindanao, but this is not the case.

At some unspecified time in the "early Pleistocene" Mindanao apparently consisted of a number of separate islands (HOOGSTRAAL 1951, 35; INGER 1954, 453 — though INGER's map is presented for Miocene conditions). If deer were present then some differentiation of populations could then have occurred. Progressive uplift of the eastern Philippines along the Samar Arc (VAN BEMMELLEN 1949, 375) no doubt brought these islands together to form the present Mindanao, but the deer populations might still retain some of their distinctions.

Pleistocene changes in sea level (MIRLIMAN and EMERY 1968) have led to the fusion and sundering of islands. It is possible that Basilan was joined to Mindanao relatively recently (INGER 1954, 455) so gene flow between "*basilaniensis*" and western populations of "*francianus*" could have occurred. This presumed genetic exchange has of course ceased, but "*basilaniensis*" could still be genotypically closer to one of the lowland Mindanao populations than they are among themselves. Such a view would find support in the contrast between the pale Buayan animals, if aboriginal, and other deer on both Mindanao and Basilan. Changing Pleistocene conditions, especially with altitudinal shifts in vegetation zones, could also explain the disjunct distribution of *C. m. nigellus* (see under that head, below).

Of course all these views are conjectural and alternative hypotheses may be equally acceptable, if not equally parsimonious. We do not know the extent to which deer distribution was influenced by their spontaneous dispersal between islands, in addition to the tectonic and isostatic events which passively separated and united populations, or the human influences that may have had similar effects. If the additional material required for more sophisticated analytical techniques becomes available, however, we might understand their history better in the future. LOWE and GARDNER (1974) for instance, have been able to distinguish native and introduced stocks of red deer, *Cervus elaphus*, in Britain using multivariate analysis of skull measurements, even though, as these authors show, the stocks are not separable taxonomically under even the most lax standards.

Localities: Mindanao, Cotabato Province: near Dadiangas, Buayan Mcpty (including Calungkingad, Neto, Olimpog, Sadsapan and Sputon) — FMNH; Tagatan (= Tatagan R.?) — AMNH, USNM; Saub — AMNH; Seranaya — USNM; Davao Province: Mapantad (Mati Mcpty) — FMNH; Kamausi (Mati Mcpty) — FMNH; Mati (Mati Mcpty) — FMNH and Heude, 1888 as type locality of *francianus*; Bukidnon Province: Mt Katanglad — FMNH; Zamboanga Province (S): Zamboanga — USNM; Lanao Province (S): Lanao — HOLLISTER, 1913; Agusan Province (S) — Mt Hilong Hilong, 900 m — SANBORN, 1953; Province not identified: Pantar —

USNM; Mt Bliss — USNM; Not traced: Catagan — FMNH; Santa Maria — USNM; Basilan — BM, FMNH — type locality of *steerii* — and HEUDE, 1888, as type locality of *basilaniensis*.

Cervus mariannus nigellus

Rusa nigellus Hollister, 1913. Mindanao, Mt Malindang.

Rusa nigellus apoensis Sanborn, 1952. Mindanao, Mt Apo.

This subspecies is significantly smaller than the Basilan and other Mindanao deer, and has a softer pelage and a higher frequency of neck-hair reversal, but in colouration seems not to be distinctive.

The male holotype of *nigellus* differs from the *apoensis* series chiefly in the more ochraceous wash on the paler parts of the body, and in the relatively long pedicles. M3 has only half erupted, so the animal is not fully adult. The antlers, which had been shed at least once, are mere spikes with incipient forks. The pedicles (measured from the orbital rim) are 73.5 mm long in *nigellus* as against 52.5–64 mm in adult and subadult *apoensis* ($n = 3$). In specimens from Cuam, adults and subadults have pedicles 61–73.5 mm ($n = 5$), but juveniles 73–96 mm ($n = 3$). In specimens from Borneo (subspecies *brookei*), the measurements are 75.5–86 mm for adults ($n = 4$), and 78–96.5 for subadults ($n = 4$), with a range of 67–102 mm in 5 juveniles. We can conclude that pedicles shorten with successive antler shedding and that the long pedicles of *nigellus* are probably not of taxonomic significance. 8 out of 9 skins from Mt. Apo, and the single skin from Mt. Malindang, have nuchal hair reversal.

Though distinctly smaller than any lowland deer, specimens from the lower slopes of Mt Apo including the holotype of *apoensis* are relatively large, intermediate between the small Buayan skulls and those from the higher elevations of Mt. Apo. There is thus every likelihood that the size reduction, the main distinction, is clinal; certainly *nigellus* is very unlikely to be a distinct species, contra SANBORN (1952).

C. m. nigellus as here revised thus has a disjunct distribution within the range of our conception of *nigricans*, but at present we see no alternative to this. It could be the result of severing of a former continuous range by upward migration of vegetation zones due to the post-Pleistocene rise in sea level; or the "subspecies" could quite simply be polyphyletic.

Localities: Mindanao: Mt. Apo (including Todaya 2800 ft; Maimit 4300 ft — type locality of *apoensis*; Meran and Sudu 6000 ft; and Baclayan 6500 ft); Mt Malindang — type locality of *nigellus*.

S u m m a r y

This paper presents a review of Philippine deer. The relevant literature is summarised. The deer fauna of each island and those of some adjacent archipelagos are identified and the status of named forms is assessed. It is concluded that *Cervus taristoeki* is a synonym of *Cervus timorensis* and that this species is absent from the Philippines; and that the name *Cervus nigricans*, though reliably associated only with the type specimen, is best regarded as the earliest name for Mindanao or Basilan deer.

Two non-rusine deer (*Cervus calamiannensis* and *Cervus cf. nippon*) are present on the Philippines. The rusine species are listed and it is concluded that there are four species altogether, *C. timorensis*, *C. unicolor*, *C. alfredi* (monotypic) and *C. mariannus* (polytypic), only the last two occurring on the Philippines, where they are endemic. The subspecies of *C. mariannus* are provisionally revised. Four forms are retained: *C. m. mariannus* (syn.

philippinus — Luzon; *C. m. barandanus* — Mindoro; *C. m. nigricans* (syn. *francianus*, *basilaniensis*, *steerii*) — lowland Mindanao and Basilan; and *C. m. nigellus* (syn. *apoensis*) — montane localities, Mindanao. Taxonomic problems concerning the last two subspecies are discussed.

Z u s a m e n f a s s u n g

Die Studie gibt eine Übersicht über die Hirsche der Philippinen. Die einschlägige Literatur wird referiert. Die Hirschfauna jeder einzelnen Insel sowie einiger angrenzender Archipele wird identifiziert und der Status der benannten Formen ermittelt. Es ergibt sich, daß *Cervus lavisiocki* ein Synonym von *Cervus timorensis* ist und daß diese Art auf den Philippinen nicht vorkommt. Der Name *Cervus nigricans*, der zuverlässig nur mit dem Typ-Exemplar in Verbindung zu bringen ist, wird am besten als der älteste Name für den Mindanao oder Basilischen Hirsch angesehen.

Zwei nicht rusine Hirsche (*Cervus calamianensis* und *Cervus cf. nippon*) kommen auf den Philippinen vor. Die Rusa-Arten werden zusammengestellt und erschlossen, daß es sich um vier Arten handelt: *C. timorensis*, *C. unicorn*, *C. alfredi* (monotypisch) und *C. marianus* (polytypisch); nur die beiden letztgenannten kommen auf den Philippinen vor, sie sind dort endemisch. Die Unterarten von *C. m. marianus* werden einer vorläufigen Revision unterzogen. Vier Formen bleiben anerkannt: *C. m. marianus* (Syn. *philippinus*) von Luzon, *C. m. barandanus* von Mindoro, *C. m. nigricans* (Syn. *francianus*, *basilaniensis*, *steerii*) von den Niederungen Mindanaos und Basilien, *C. m. nigellus* (Syn. *apoensis*) gebirgisches Gelände Mindanaos. Taxonomische Probleme der letztgenannten zwei Unterarten werden erörtert.

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