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Oliver A. Ryder
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TESTING RHINOCEROS SUBSPECIES BY MULTIVARIATE ANALYSIS

Colin P. Groves
Australian National University, Canberra

INTRODUCTION

Subspeciation in rhinoceroses is today not merely of interest for what it tells us about phylogenetic and biogeographic patterns, but of considerable importance in conservation planning. It is in principle desirable to save as many demes (local gene-pools) of a species as possible, but in some cases, especially in the case of the Black Rhinoceros, *Diceros bicornis*, most of these local populations are so reduced that there is no possibility of saving them all. So subspecies, the lowest formal level of taxonomy, must suffice as the unit of conservation, as far as even that is feasible.

In a series of papers (Groves, 1965; Groves, 1967a; Groves, 1967b; Groves, 1975; Rookmaaker & Groves, 1978; Gurin & Groves, 1980; Groves & Chakraborty, 1983) colleagues and I have proposed to divide up four of the five living rhinoceros species into subspecies. The only monotypic species would be *R. unicornis*. Some of these proposals were based on material that was less than adequate for really definitive analysis (see, for example, Du Toit, 1986, who proposes guidelines for a reappraisal of *Diceros bicornis* subspecies), but was none the less all that was available at the time.

It certainly high time to reexamine at least the three species (*Rhinoceros sondaicus*, *Dicerorhinus sumatrensis*, *Diceros bicornis*) for which some further material has accumulated since the above publications, and also *Rhinoceros unicornis* which has never been investigated taxonomically. The easy availability of advanced statistical packages since the mid-1980s makes some form of multivariate analysis ideal for this purpose.

MATERIAL AND METHODS

The original samples of *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis* were described in Groves (1965, 1967a) and Groves & Chakraborty (1983); further material has been measured in the Museum Zoologici Bogoriense, the Sarawak Museum, the Melaka Zoo and the private collection of Mr. Chokchai Bulukul in Bangkok. I am most grateful to Bp. Boeadi, Dr. Lucas Chin, Encik Zainal-Zahari Zainuddin, and Dr. Boonsong Lekagul for their kind assistance in showing me this material. Dr. Guy Musser kindly sent me measurements of a previously unexamined skull in the American Museum of Natural History.

Skulls of *Rhinoceros unicornis* were measured in the Natural History Museum, London, and the Zoologisches Institut, Hamburg. I am most grateful to Dr. Juliet Clutton-Brock and Prof. Dr. Harald Schliemann for their assistance in these cases.

Further skulls of *Diceros bicornis* were measured at the following institutions: Naturhistoriska Riksmuseet, Stockholm; Naturhistorisches Museum, Bern; Zoologisches Museum, Berlin; Koninklijk Museum voor Middenafrika, Tervuren; Landessammlung fr Naturkunde, Karlsruhe; private collection of the Maharaja of Baroda; Zoologisches Staatssammlung, Munich; Zoologisches Museum, Bonn; Senckenbergisches Museum, Frankfurt; Kenya National Museum, Nairobi; Arusha National Park; Serengeti Research Institute; Institut voor Taxonomisch Zoologie, Amsterdam; Museo Lo Speccola, Florence; private collection Ms. Jenny Horne, Nairobi; Mweka College, Moshi; Universitets Museum, Copenhagen; Powell-Cotton Museum, Birchington; Naturhistorisches Museum, Vienna; Zoology Museum, Cambridge; Musum National d'Histoire Naturelle, Paris; Muse d'Histoire Naturelle, Marseille. I am most grateful to the curators of all these institutions for their kindness and assistance. Finally, I am most grateful to Dr. Harald Roth and Dr. Vivian

-Wilson for sending me measurements of skulls in the Zimbabwe National Museum, Bulawayo.

Analysis used the Discriminant Functions program of SPSS-X. Discriminant Functions (or Canonical Variates) compares predetermined groups with each other, maximising between-groups variation compared to within-groups variation, and reorganising the original variables into a number of uncorrelated ones (=the Discriminant Functions), such that the maximum amount of discriminating power resides in the first Function, folowed by the second, and so on to the nth.

DICEROS BICORNIS

The following variables were used in the analysis: Greatest (skull) Length, Basal Length, Bizygomatic Breadth, Postorbital (constriction) Width, Occipital (crest) Breadth, Occipital Height (opisthion to inion), Nasal (boss) Breadth. Use of all these variables reduced the number of skulls available for analysis to 87; some skulls were incomplete at critical points, and (more important) others were measured at times in the past when the full measuring schedule was not to hand. A second analysis was run omitting Postorbital Width, the variable most usually missing; now, 103 skulls were available for analysis.

The groups made for the analysis were not always large enough to warrant inclusion, so some were cancelled. The remaining groups were as follows:

No.	Region	n
2	Kariba	12
3	Luangwa	5
6	Karagwe	7
7	Arusha and Kilimanjaro	11
8	Serengeti, Olduvai and Eyasi	21
0	Tsavo	6
D	Archer's Post and northern Guaso Nyiro	3
F	Ogaden and Jubaland	5
H	Atbara region and Eritrea	6
I	Chad and Central African Republic	9

The second analysis, dropping Postorbital Width, permitted the addition of a Group 9, Southern Guaso Nyiro; and increased the number of skulls in some of the other groups - in particular, Group D now totalled 9 skulls instead of 3.

In addition, a few individual specimens were entered as "ungrouped", to see where they might fall in relation to the groups on which the dispersion was based: one each from Angola, Tanga, Umba River, Berbera (neotype of *somaliensis*), Lake Baringo, Shambe (S.E. Sudan, type of *ladoensis*) and Aveng (S.W.Sudan, type of *palustris*); two each from Southeast Tanzania and Katanga; and four from the Chobe River (*D.b. chobiensis*). These last were entered individually, rather than as a group, in case their very large size skewed the analysis in favour of being size-based, rather than shape-based. The second analysis, omitting Postorbital Width, enabled a second Baringo skull to be entered, as well as three from the upper Tana River region.

Figure 1 plots Discriminant Function 1 (horizontal) against DF2 (vertical) for the full variable list. DF1, which accounts for 44% of the total variance, is not highly correlated with any of the original variables; the highest correlations are with Occipital Height (positive) and Occipital Breadth and Bizygomatic Breadth (negative). DF2, which accounts for 20% of the variance, has fairly high positive correlations with Basal Length and Bizygomatic Breadth.

There is a central cluster, representing the large Group 8 (Serengeti region). Group 2 (Kariba) falls away from the central cluster to the left side, and Group 3 (Luangwa) to the right, in each case with only a small overlap. Group 7 (Arusha) extends through both the Group 8 and Group 2 clusters; Group 6 and Group H overlap with Group 8, but extend somewhat beyond it towards the right of the diagram. Groups O (Tsavo), D (Archer's Post), F (Ogaden) and I (Chad) fall largely or entirely within the range of Group 8.

As far as the ungrouped specimens go, one from Katanga, three from Chobe, and the skulls from Tanga, Baringo, Angola, Shambe and southeast Tanzania fall within the boundaries of Group 2, or in its overlap zone with Group 8; Umba, and one each from Katanga and Chobe fall within the Group 8 dispersion. Aveng falls within Group 3, and Berbera outside any group (it is the "pound sterling sign" in the general vicinity of the outliers of groups 6 and H).

Using the subspecific categories of Groves (1967b), the central dispersion contains *D.b. michaeli* and *longipes*, the left-hand one *D.b. minor*; the right-hand one, Group 3, is a population which was inferentially included in *D.b. minor*, apparently incorrectly as it now turns out. *D.b. brucii* overlaps extensively with the michaeli cluster; *D.b. chobiensis* and *ladoensis* with both *michaeli* and *minor*. The population from the Arusha region would seem to be intermediate between the two (in agreement with Groves, 1967b). No specimen of the gigantic extinct *D.b. bicornis* was entered into the analysis. (It should be pointed out that specimens from Zululand, the type locality of *D.b. minor*, were too few in number to be entered in the analysis; consequently, it is not absolutely certain that the Kariba sample does truly represent that putative subspecies).

Inspection of the values for the remaining Discriminant Functions (3 to 7) failed to reveal any particularly striking patterning. The analysis performed without Postorbital Width nearly duplicated the first analysis, except that Groups 2 and 8 were less distinct from each other.

These results should not be taken as evidence for combining *D.b. longipes* and *brucii* with *D.b. michaeli*: they differ in other respects (Groves, 1971; Rookmaaker & Groves, 1978). There does seem, however, some support for the idea mooted in Groves (1967b) that, in some respects, *ladoensis* and *somaliensis* are connected by clinal gradations with *D.b. michaeli*: the Baringo specimens, in Fig.1, are intermediate between Group 8 and the Shambe skull, type of *ladoensis*, and the Ogaden specimens (Group F) link the neotype of *somaliensis* with Group 8. Whether it is still worthwhile maintaining *ladoensis* as a distinct subspecies is perhaps disputable; though *brucii* (senior synonym of *somaliensis*) would still be worth recognising as the Ogaden specimens show the distinctive dental characters as well as do more northerly (craniometrically extreme) specimens.

The most unexpected result is the striking separation of the Luangwa valley sample (Group 3): though there are not many specimens, their clear distinction from all others (except the Aveng skull from Sudan!) implies that there should be further intensive study to elucidate their position - whether they deserve separate subspecific status. This would be especially important as the population still exists in apparently viable if very low numbers.

DICERORHINUS SUMATRENSIS

The following measurements were used: Occipitonasal Length, Basal Length, Bizygomatic Breadth, Nasal (boss) Breadth, Occipital (crest) Breadth, Occipital Height, Interorbital (constriction) Width, and Preorbital (convexity) Breadth. The Groups were as follows:

Group 1, Borneo:	n=7
Group 2, Sumatra:	n=13
Group 3, Malay peninsula:	n=7
Group 4, N.Burma and "India":	n=2
Group 5, Pegu and Thailand:	n=2

The results of the analysis (Fig.2) are wholly in accord with Groves (1967a): Borneo (*D.s. harrissoni*), Sumatra plus Malaya (*D.s. sumatrensis*) and Burma/India (*D.s. lasiotis*) are quite separate, the latter being linked clinally to Sumatra/Malaya by Pegu (and Thailand: new material since the 1967a study). Though DF1 (51% of the variance) is positively correlated with most of the original variables, it does not represent size alone, as the only strong correlations are with Bizygomatic Breadth and Interorbital Width. DF2 (32% of the variance) is most strongly (negatively) correlated with Occipital Breadth.

Though the subspecific identity of Sumatran and Malayan populations is supported, it should be noted that an average difference does remain: the gene pools should as far as possible be kept separate in the breeding program.

RHINOCEROS SONDAICUS

The following variables were used in the analysis: Occipitonasal Length, Bigyomatic Breadth, Nasal (boss) Breadth, Occipital (mastoid) Width, Occipital Height, Interorbital (constriction) Width, Preorbital Width. Note that Basal Length could often not be measured as the failure of the premaxillae to fuse with the maxillae until extreme old age, characteristic of this species, meant that premaxillae were actually lost in many skulls. Two analyses were run, one without and one with Preorbital Width. The numbers of skulls were as follows:

Group	Locality	n (An. 1)	n (An.2)
1	Java	15	13
2	Sumatra	6	5
3	Malaya	2	
4	Vietnam	4	3
5	Sunderbans (Bengal)	4	4

There were also three ungrouped skulls: two from Tenasserim (peninsular Burma) and one of uncertain locality (the Indian Museum skull collected by Wallich: see Groves & Chakraborty, 1983).

Figure 3 shows the results of the first analysis (more specimens, fewer variables). DF1 (53.5% of the variance) is most strongly (positively) correlated with Bizygomatic Breadth; DF2 (32% of the variance) with Occipitonasal Length and Interorbital Width. Java, Sumatra, Malaya and Vietnam ranges overlap, but Bengal remains separate. One of the Tenasserim skulls falls outside the range of all others (in the opposite direction to the two larger mainland groups); the other falls within both Java and Vietnam dispersions. The Wallich specimen falls in the overlap zone between Java and Sumatra.

Figure 4 shows the results of the analysis run with Preorbital Width included (hence fewer specimens available). DF1 (62% of variance) is this time positively correlated with Occipital Height as well as with Bizygomatic Breadth, and DF2 (29% of variance) has the same positive correlations as in the first analysis and, in addition, a negative correlation with Nasal Breadth. This time Groups 1 and 2 overlap less (but still substantially), Group 4 is now quite distinct from other groups, and Group 5 is well individualised. The (single remaining) Tenasserim skull is even further from the groups, and the Wallich skull is closest to Group 4 (Vietnam), though it could be an outlier to Sumatra/Java.

The three-subspecies model of Guerin & Groves (1980) and Groves & Chakraborty (1983) seems to be supported by this analysis. At any rate, *Rhinoceros sondaicus inermis*, the extinct Sunderbans form, was thoroughly distinct from all others.

The same measurements were used for the analysis as for the second *R. sondaicus* analysis, with Basal Length in addition. There were only two groups: Assam (Group 1), 6 specimens, and Nepal (Group 2), also 6 specimens, with a Kuch Behar specimen remaining ungrouped.

With only two groups, there was only a single Discriminant Function, which was positively correlated with Interorbital Width, Occipital Breadth and Preorbital Breadth, and negatively with Bizygomatic Breadth. The result (Fig.5) was completely unexpected: the two groups separately cleanly, with the Kuch Behar skull falling at the edge of the Nepal group.

DISCUSSION

The category of subspecies is still of value in mammalian systematics, provided one does not "reify" it and as a consequence overlook the significance of gene-pools that are fairly distinctive but fail to reach conventional levels of subspecific differentiation. It seems likely that in *Dicerorhinus sumatrensis* and *Rhinoceros unicornis*, existing local (insular or quasi-insular) gene-pools can still be saved and kept separate (with the possible exception of *Dicerorhinus sumatrensis lasiotis*). In *Rhinoceros sondaicus* only two of these gene-pools still exist, and they are probably, as corroborated by this analysis, subspecifically distinct anyway. In *Diceros bicornis*, the remnants of many of the local populations will have to be, or have already been, amalgamated, and subspecies will serve as a guidelines for these amalgamations; much more study is still needed in this species, despite the advances made by possible by multivariate analysis, and the proposals of Du Toit (1986) remain relevant.

Several lines of action as far as *Diceros bicornis* taxonomy is concerned seem required by the present analysis. The first is the description, after further thoroughgoing study, of the Luangwa Valley (Zambia) population as a separate subspecies. This would increase the number of subspecies to 8, unless it be deemed unnecessary to maintain *D.b. ladoensis*, being a clinal variant of the large East African subspecies. Skulls from Zululand need to be measured to ascertain precisely what *D.b. minor* actually is; and skulls from various parts of East, Southeast and Southwest Africa must be compared to both Zululand and Kariba samples to decide just which populations are *D.b. minor* and which are not. The next analysis, based one hopes on more and larger samples, should leave ungrouped the skulls here lumped as Group 7 (Arusha), as inferentially this sample spanned the border between *D.b. michaeli* and "*minor*". Dental characters now appear to vary geographically within the species to a greater extent than was formerly appreciated (Rookmaaker & Groves, 1978), and it may turn out that no East African rhinos are actually *D.b. minor*.

Postcranial skeletons are of significance too: available photographs of *D.b. longipes* certainly make it look long-legged, but the proposition needs to be tested with actual specimens. The horn character attributed to this subspecies by Zukowsky (1949) was supported on the basis of a single specimen by Groves (1971), and a further specimen seen in the Marseille Museum again has the character (very markedly so, in fact); but this too requires testing on further material.

Dicerorhinus sumatrensis is, as expected, divided into three quite distinct subspecies, but the northern one, *D.s. lasiotis*, is in effect a clinal extreme of the nominotypical *sumatrensis*. Within *Rhinoceros sondaicus*, three subspecies seem certainly worth maintaining; it is a great pity that the distinctive Sunderbans form has been extinct for nearly a century.

On the evidence presented here, it would seem necessary to divide *Rhinoceros unicornis* into two subspecies (both of which, fortunately, still exist in reasonable quantity). Lydekker (1916) would appear to have formally fixed the type locality of the species as "probably the sub-Himalayan Tarai of Assam"; unfortunately the only other names associated with any locality (*Rhinoceros jamrachi* Jamrach, 1875, and *Rhinoceros unicornis bengalensis* Kourist, 1970, both based on a living specimen from Manipur: see Rookmaaker, 1983) are also from the eastern end of the distribution. There is no available name for a Nepalese subspecies; a

name could be provided at this time, but further material would be preferable to put it on a really firm basis.

CONCLUSIONS

In general, described subspecies in the four rhino species here studied are maintained in multivariate analysis. New subspecies of *Diceros bicornis* (from Luangwa Valley) and of *Rhinoceros unicornis* (from Nepal) seem indicated.

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Fig.1. Diceros bicornis

DF 1 (horizontal) - 44% of variance
DF 2 (vertical) - 20% of variance

Fig.2. Dicerorhinus sumatrensis

DF 1 (horizontal) - 50.9% of variance
DF 2 (vertical) - 31.7% of variance

ALL-GROUPS SCATTERPLOT - * INDICATES A GROUP CENTROID   Reduced variable list

CANONICAL DISCRIMINANT FUNCTION 1

1 - Java
2 - Sumatra
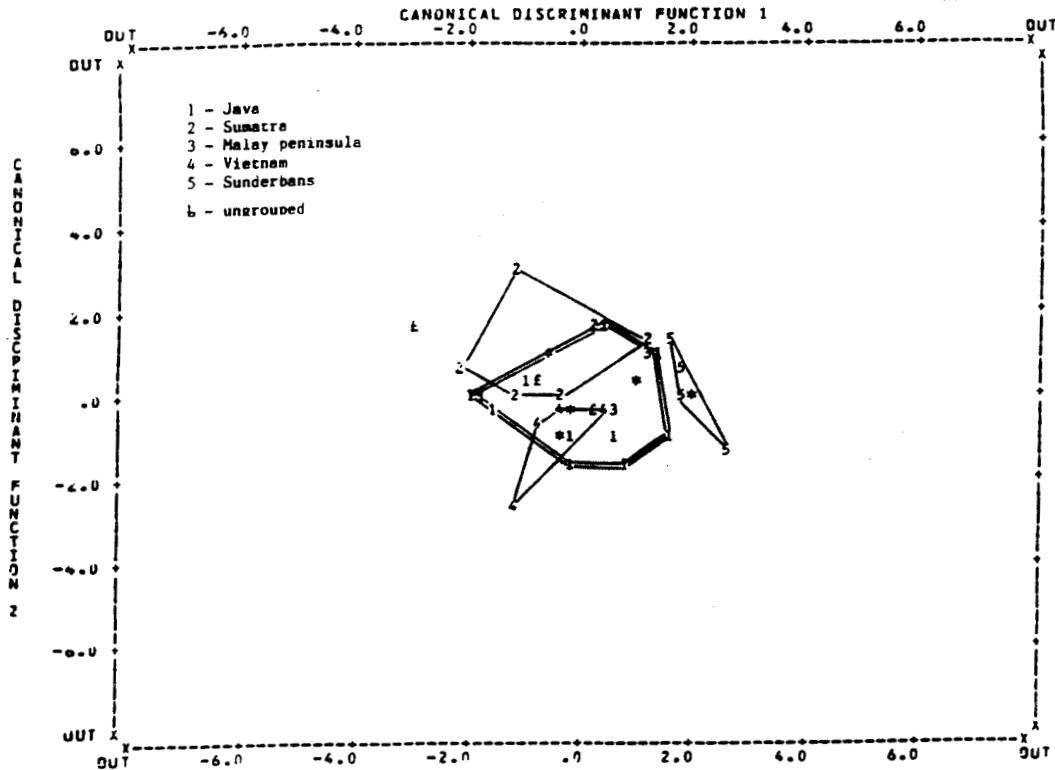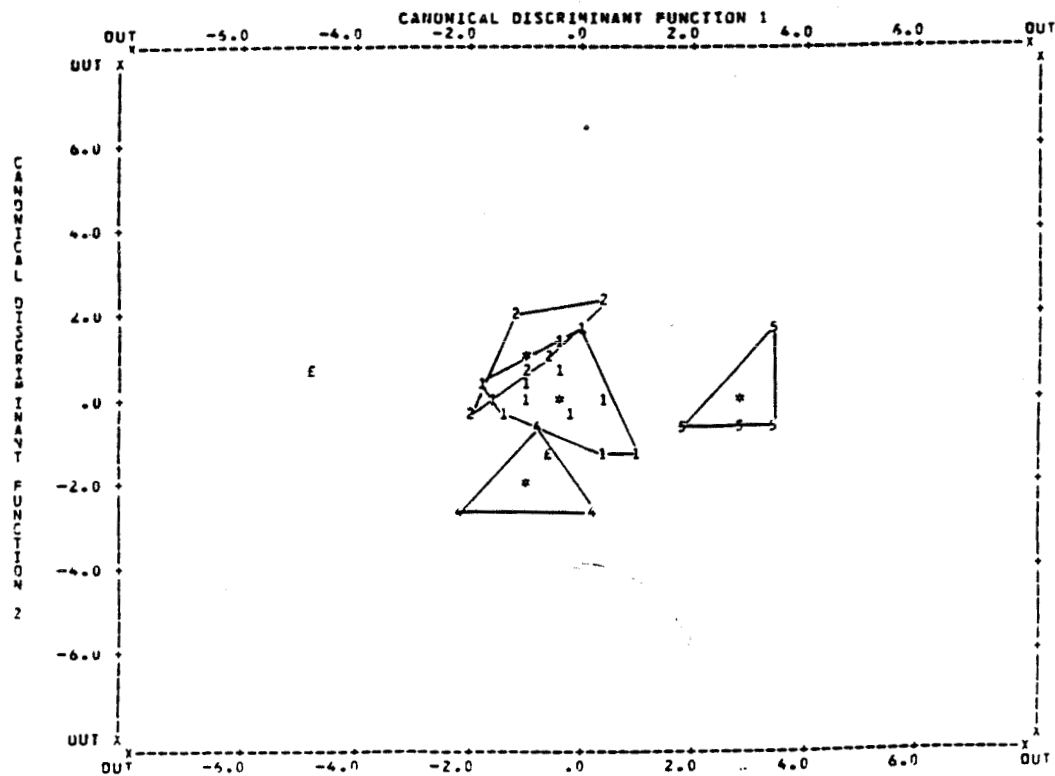3 - Malay peninsula
4 - Vietnam
5 - Sunderbans

6 - ungrouped

Fig.4. Rhinoceros sondaicus

DF 1 (horizontal) - 62% of variance
DF 2 (vertical) - 29% of variance

Full variable list: key as Fig.3

ALL-GROUPS SCATTERPLOT - * INDICATES A GROUP CENTROID

CANONICAL DISCRIMINANT FUNCTION 1

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                        ALL-GROUPS STACKED HISTOGRAM
                       CANONICAL DISCRIMINANT FUNCTION 1

     4 +                                                                                    +
F        |     1 - Assam                                                                    |
R    3 + |     2 - Nepal                                                                    +
E        |                                                                                  |
Q        |     b - Kuch Behar (ungrouped)                                                   |
U    2 + |                                          2                                        +
E        |                                          2                                        |
N        |                                          2                                        |
C    1 + |                              222 2 2 E    1 1 1    1 1      1                      +
Y        |                              222 2 2 E    1 1 1    1 1      1                      |
         |                              222 2 2 E    1 1 1    1 1      1                      |
         |                              222 2 2 E    1 1 1    1 1      1                      |
       X-----------+---------+---------+---------+---------+---------+---------+---------X
     OUT         -6.0      -4.0      -2.0       .0       2.0       4.0       6.0      OUT
CLASS    2222222222222222222222222222222222222222222222221111111111111111111111111111111111111111
CENTROIDS                                        2         1
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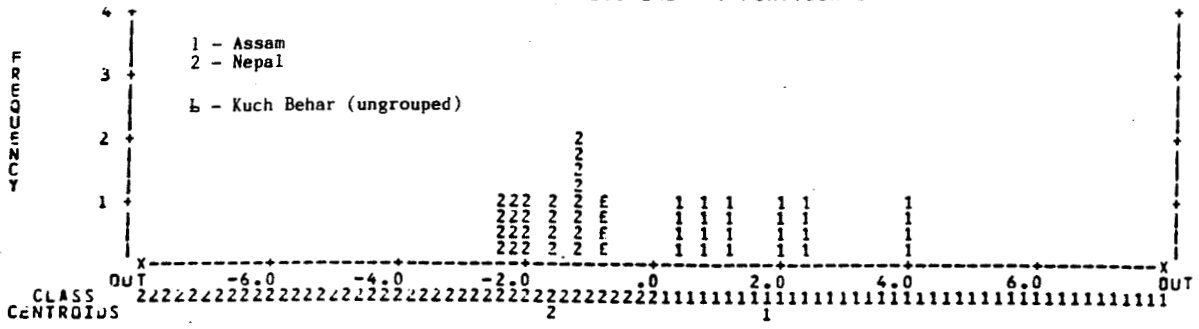
Fig.5. <u>Rhinoceros</u> <u>unicornis</u>