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The subspecific division of *Rhinolophus luctus* Temminck, 1835, and the taxonomic status of *R. beddomei* Andersen, 1905 (Mammalia, Chiroptera)

by
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Abstract: The subspecific division of *Rhinolophus luctus* Temminck, 1835 is reviewed, and the taxonomic status of *Rhinolophus luctus beddomei* (Andersen, 1905) is discussed. Specimens in the Bombay Natural History Society, The Natural History Museum, London, and a recently collected Vietnamese animal are statistically analysed. The South-Indian *Rhinolophus beddomei* is regarded as different from *Rhinolophus luctus* at specific level.
Key words: taxonomy, systematics, morphometrics, Oriental Region, *Rhinolophus*.

Introduction

The species *Rhinolophus luctus* Temminck, 1835 is the largest known form in its genus. It is also among the rarest horseshoe bats due to its solitary habits, found singly or in pairs, and therefore it is rare in collections. Besides this species, a number of closely related forms have been made known to science during the past century and a half.

The typical race comes from Java and another form described as a separate species *R. morio* Gray, 1842 from Singapore. The apparently most common form with the most extended range, *R. l. perniger* Hodgson, 1843 was named from Nepal.

Later, several other forms were described from 1905 onwards. Andersen (1905a, 1905b, 1918) introduced *R. lanosus* from NW Fokien, China, *R. geminus* from Java, *R. morio foetidus* from Borneo, *R. beddomei* from Mysore, India, *R. beddomei sobrinus* from Sri Lanka. Andersen (1905a) noted that *R. geminus* was much nearer the Himalayan form (*R. perniger*) than to *R. luctus* living in Borneo and the Malay Peninsula. He also remarked under *R. luctus* p. 252: "If by further examination Java specimens should prove to differ from Borneo-Malacca form, the former will have to stand as *Rh. luctus*, the latter as *Rh. morio* Gray", further: "in every other respect" (other than colour) "*Rh. morio* is indistinguishable from Selangor and Borneo specimens". G. Allen (1928) described *R. lanosus spurcus* from Hainan, China. He gave for the skull measurements of *R. l. spurcus* (p.3) about as great values as those of true *R. l. perniger* when he stated them to be greater than those of *R. lanosus*. Sanborn (1939) published *R. formosae* from Taiwan. Chasen (1940) synonymized *R. l. geminus* with *R. luctus* and confined the latter to Java and part of Sumatra, and regarded both *R. morio* (distributed in the Malay Peninsula and part of Sumatra), and *R. foetidus* (Borneo) as separate subspecies of *R. luctus*. Tate (1943), Tate & Archbold (1939) appeared to regard all named forms as subspecies of *R. luctus* (see also Ellerman & Morrison-Scott 1951,

p. 121), although they remarked "their treatment as races is provisional"..and ..."A detailed and painstaking analysis with a large quantity of material will be required before the races of *R. luctus* can be worked out satisfactorily" (Tate 1943 p. 5).

It is somehow strange that Tate (1943), while retaining Andersen's original "groups", put *R. pearsoni* in the *R. luctus* group and thus - in a later sense - as a subspecies of the latter. Well after that, *R. pearsoni* was recognized as a clearly distinct species by Ellerman & Morrison-Scott (op. cit.). (Incidentally, the specimen of *R. l. perniger* deposited in the Hungarian Natural History Museum, was found in the same cellar as a small colony of *R. pearsoni* at Tam Dao in Vietnam by the present junior author.)

Sinha (1973) gave details on the material in the Calcutta collection of the Zoological Survey of India. Lekagul & McNeely (1977) considered "probably two subspecies in Thailand: *R. l. luctus* in the south as far north as Tenasserim, and perhaps *R. l. perniger* in the north". Payne *et al.* (1985) briefly discussed the ecology and habitat of *R. l. foetidus* and reported it from lowlands up to 1600 m in the mountains of Borneo. Liang & Dong (1984) and Chen *et al.* (1989) reported the species from further localities in Southern China. Ando *et al.* (1983) studied the karyotype of the species from Taiwan, Narayana Naidu & Gururaj (1984) in India, and Harada *et al.* (1985) the same topic in the specimens from Thailand.

Materials and methods

During the rather intensive collectings of bats by the senior author in India, this bat (*R. beddomei*) was seen but once in Southwestern India. The species and the South-Indian *R. beddomei* were studied briefly (by the senior author) in the Bombay Natural History Society's collection where there were available 6 specimens of *R. l. beddomei*, 6 specimens of *R. l. perniger* and 1 specimen of *R. l. lanosus* in 1967. The female *R. l. perniger* obtained by the junior author is the third known specimen from northern Vietnam, the first two were collected at the same locality and deposited in the Institute of Systematics and Evolution of Animals, Krakow, Poland (Cao Van Sung in litt.).

Skulls of thirty specimens of *Rhinolophus luctus* (s.l.) were used for the present study. List of the specimens with names of subspecies (*R. l. perniger*, *R. l. morio*, *R. l. foetidus*, *R. l. beddomei*), serial number for the present study, location of the specimen (Hungarian Natural History Museum, Budapest = HNHM, The Natural History Museum, London = BNHM, Bombay Natural History Society, Bombay = BNHS), register No., sex (male = m, female = f, undetermined = s?), and collecting locality as follows.

R. l. perniger: 1:HNHM 11111, f, Tam Dao, Vietnam; 2:BNHM 78.2310., m,Chiangmai, Thailand; 3:BNHM 7.1.1.294., s?, "Calcutta", India(?); 4:BNHM 9.10.11.2., s?,Chiangmai, Thailand; 5:BNHM 21.1.6.4., m, Khonshong, Jaintia Hills, Meghalaya, India; 6:BNHM 21.1.6.5., m, Khonshong, Jaintia Hills, Meghalaya, India; 7:BNHM 79.11.21.142., s?, Masuri (Mussoorie), Uttar Pradesh, India; 8:BNHM 79.11.21.141., m, Masuri (Mussoorie), Uttar Pradesh, India; 9:BNHM 9.1.4.11., m, Darjeeling, West Bengal, India; 10:BNHM 91.10.7.55., s?, Sikkim; 11:BNHM 23.1.9.1., f, Chalma-Khel, Nepal; 12:BNHM 21.1.6.2., Bankochori, S.Tenasserim, Burma; 13:BNHM 21.1.6.3., Kindat, Chin Hills, Burma; 14:BNHM 50.396., f, Nam Tamas Valley, Upper Burma; 15:BNHM 50.397., f, Taron Valley, Upper Burma; 16:BNHM 21.1.6.1., m, Sokteik, N.Shan State, Burma; 17:BNHS 3073, f, Khonshong, Jaintia Hills, Meghalaya, India; 18:BNHS 3072, m, Khonshong, Jaintia Hills, Meghalaya, India; 19:BNHS 3071, f, Bouzini, Nepal.

R. l. morio: 20:BNHM 1.3.9.3., s?, Semangko Gap, Selangore, Malaysia; 21:BNHM 78.2309., f, Pak Thengchai, Sukerat, Thailand; 22:BNHM 70.1463., f, Korat Pn, Thailand.

R. l. foetidus: 23:BNHM 76.9.20.12., s?, N.W.Borneo; 24:BNHM 92.2.7.3., f, Mt.Dulit, Borneo; 25:BNHM 94.9.29.4., s?, Mt.Dulit, Borneo; 26:BNHM 98.11.3.9., s?, Lawas, Borneo; 27:BNHM 59.183., f, Lobang Badak, Serabang, Borneo.

R. l. beddomei: 28:BNHM 12.11.28.5., m, Sirsi, N.Kanara, Karnataka, India; 29:BNHM 11.3.16.1., f, Konkan, Maharashtra, India; 30:BNHS 3081, m, Karla Caves, Pune, Maharashtra, India.

Specimen with registration no. 70.1463. from Central Thailand in the BNHM was identified as *R. l. perniger*, however, according to J.E. Hill's notes on its label made in 1974 "*perniger* but small and tends to *morio*". Another specimen (73.2310.) from N. Thailand was identified as *R. l. perniger* with question mark on its label and placed in a box with specimens of *R. l. morio*.

Only 14 measurements of the above mentioned three *R. l. perniger* and one *R. beddomei* in the Bombay Natural History Society collection (BNHS) were taken with the help of a vernier caliper. Except when a skull was fragmentary, all the other specimens were measured for a total of 38 cranial and dental characters with a "Digimatic" caliper to 0.01 mm accuracy. A series of measurements, especially those of short distances and teeth were measured with the caliper under a stereomicroscope. Abbreviations of the measurements used in the paper along with explanations are as follows.

C–CONDYL	condylar length of skull (from front of canines to back of condyles)
TOTAL–LE	total length of skull (from front of canines to occiput)
BASIL–LE	basilar length of skull (from frontal edge of palate [without praemaxillae] to the foremost part of ventral incision between condyles)
ZYG–WIDT	width of skull between zygomata
MAST–WID	mastoid width of skull (between mastoid knobs)
C–C–WIDT	width of rostrum between outer margins of crown of canines
M3–M3–WI	width of rostrum between outer crowns of M^3s
UC–M3–LE	crown length of upper C-M^3
PALBRI–L	length of palatal bridge (without the posterior spike)
COCH–DIS	distance between cochleae
BRCASE–W	width of braincase (just above mastoid knob)
BRCASE–H	height of braincase (from base to top with sagittal crest)
LACFOR–W	width of rostrum between lacrimal foramina
UC–P4–LE	crown length of upper C-P^4
UM1–M3–L	crown length of upper M^1-M^3 (from the anteriormost portion of parastyle of M^1 to the posteriormost edge of protocone of M^3)
UC–BLENG	basal cross-sectional length of upper C
UC–WIDTH	basal cross-sectional width of upper C
UM1–LENG	antero-posterior length of upper M^1 (between parastyle and metastyle)
UM1–WIDT	width of upper M^1 (between lingual base of protocone and labialmost edge of mesostyle)
UP2–LENG	antero-posterior crown length of upper P^2
UP2–WIDT	crown width of upper P^2
BULLA–LE	greatest length of bulla
MAND–LEN	length of mandible (between hindermost portion of articular process and anteriormost edge of I_1 alveolus)
LC–M3–LE	crown length of lower C-M_3
LC–P4–LE	crown length of lower C-P_4 row
LM1–M3–L	crown length of lower M_1-M_3 (between anterior edge of paraconid of M_1 and posterior margin of hypoconulid of M_3)
PR–COR–H	height of coronoid process (between its top and the sinus on ventral profile of mandibular body)
LP4–LENG	length of lower P_4 (between its paraconid and hypoconulid)
LP4–WIDT	greatest basal width of lower P_4
LP2–LENG	greatest basal length of lower P_2
LP2–WIDT	greatest basal width of lower P_2
LM1–LENG	length of lower M_1 (between its paraconid and hypoconulid)
LM1–TA–W	talonid width of lower M_1
LM3–LENG	length of lower M_3 (between its paraconid and hypoconulid)
LM3–TA–W	talonid width of lower M_3
INTERO–W	width of interorbital constriction
NAKNOB–W	width of nasal knob
NAKNOB–H	greatest height of nasal knob (from palate to top)

For the statistical analyses of the available variables the SYSTAT statistical computer programme package (Wilkinson 1990) was used.

Results and discussion

There were noted the following differences between *R. l. perniger* (3073, Jaintia Hills, Figs 1, 2, 3) and *R. l. beddomei* (3081,Pune, Figs 4, 5, 6) in the Bombay Society's collection.

The skull of *R. beddomei* is found to be much smaller with relatively greater zygomatic width, with much shallower hollow above the interorbitalia. The backward-curving hook of premaxilla is shorter and thus the central hole is not closed as in *R. l. perniger*. The premaxillae join the maxillary palate with an absolutely wider base than in *R. l. perniger*. The opening of the choana between pterygoids, that is, the palation is identical to the one in the other form, however, smaller. The bulla tympani in *R. beddomei* is less inflated. The upper toothrows of *R. beddomei* are anteriorly nearer to each other. The upper C and P^4 are of smaller basal cross-section, apparently because of their less developed cingula in *R. beddomei*. The upper C of *R. beddomei* on its extero-posterior base has no impression for P^2 as in *R. l. perniger*. As regards the differences in the mandibles of the two forms, the coronoid process seems more narrowely pointed in the smaller mandible of *R. beddomei*. The lower C is antero-posteriorly more shortened and also the P_4 is much shorter than in *R. l. perniger*. The less sloping labial cingulum of the latter is but with a slight wave in *R. beddomei*. The talonid of M_3 of *R. beddomei* is much wider and also wider than its trigonid, just opposite to the case in *R. l. perniger*.

The authors recently studied the skulls of the available specimens (except types) in the collection of The Natural History Museum, London (Figs 7, 8, 9) and the skull of the specimen in the Budapest collection from Vietnam (Figs 10, 11). Disregarding the few specimens from Thailand, collected in the seventies, the collection of the skulls in London is about the same as in Andersen's time.

Statistical data

Generally speaking, especially the cranial measurements of *R. beddomei* are smaller than those of others as shown by the basic statistical data (see Tables 1, 2, 3,).

Table 1. Basic statistical data of *R. beddomei*, total observations: 3

	C–CONDYL	TOTAL–LE	BASIL–LE	ZYG–WIDT	MAST–WID
N. OF CASES	3	3	3	3	3
MINIMUM	23.410	26.650	17.790	13.810	12.000
MAXIMUM	24.550	27.800	18.690	14.200	12.470
C–C–WIDT	M3–M3–WI	UC–M3–LE	PALBRI–L	COCH–DIS	BRCASE–W
3	3	3	3	2	2
7.260	9.710	10.130	3.900	0.790	10.550
7.590	10.200	10.490	4.700	0.890	11.450
BRCASE–H	LACFOR–W	UC–P4–LE	UM1–M3–L	UC–BLENG	UC–WIDTH
2	2	2	2	2	2
7.910	5.640	4.620	6.280	2.100	1.780
8.020	5.680	4.870	6.330	2.160	1.940
UM1–LENG	UM1–WIDT	UP2–LENG	UP2–WIDT	BULLA–LE	MAND–LEN
2	2	2	2	2	3
2.230	2.750	0.550	0.670	4.190	18.500
2.350	3.050	0.710	0.760	4.270	18.860

Table 1. cont.

LC–M3–LE	LC–P4–LE	LM1–M3–L	PR–COR–H	LP4–LENG	LP4–WIDT
3	2	2	2	2	2
10.920	4.040	6.870	4.690	1.500	1.430
11.070	4.100	7.060	4.780	1.590	1.530
LP2–LENG	LP2–WIDT	LM1–LENG	LM1–TA–W	LM3–LENG	LM3–TA–W
2	2	2	2	2	3
1.210	1.100	2.350	1.810	2.170	1.640
1.310	1.210	2.360	1.900	2.360	1.710
INTERO–W	NAKNOB–W	NAKNOB–H			
2	2	3			
2.500	7.010	5.200			
2.630	7.260	5.620			

Table 2. Basic statistical data of *R. l. perniger*, total observations: 19

	C–CONDYL	TOTAL–LE	BASIL–LE	ZYG–WIDT	MAST–WID
N. OF CASES	15	17	14	16	16
MEAN	27.811	31.195	21.308	15.363	13.728
STD DEV.	0.617	0.842	0.594	0.768	0.275
MINIMUM	26.650	29.700	20.420	13.270	13.200
MAXIMUM	28.800	32.550	22.400	16.450	14.120
C–C–WIDT	M3–M3–WI	UC–M3–LE	PALBRI–L	COCH–DIS	BRCASE–W
17	18	19	17	12	13
8.555	10.940	12.125	4.891	0.773	12.053
0.321	0.368	0.375	0.367	0.174	0.357
8.080	9.960	11.490	4.300	0.460	11.540
9.130	11.720	12.900	5.600	1.110	12.830
BRCASE–H	LACFOR–W	UC–P4–LE	UM1–M3–L	UC–BLENG	UC–WIDTH
12	15	16	16	16	16
8.599	6.641	5.692	7.138	2.653	2.252
0.386	0.235	0.254	0.237	0.180	0.141
7.980	6.260	5.240	6.810	2.340	2.030
9.260	7.180	6.110	7.540	3.000	2.520
UM1–LENG	UM1–WIDT	UP2–LENG	UP2–WIDT	BULLA–LE	MAND–LEN
16	16	16	16	13	17
2.686	3.028	0.853	0.999	4.724	22.252
0.110	0.194	0.137	0.087	0.196	0.549
2.550	2.670	0.580	0.780	4.460	21.100
3.010	3.350	1.070	1.100	5.050	23.280
LC–M3–LE	LC–P4–LE	LM1–M3–L	PR–COR–H	LP4–LENG	LP4–WIDT
19	16	16	14	16	16
13.003	5.198	7.893	5.456	1.826	1.671
0.406	0.209	0.261	0.373	0.092	0.148
12.350	4.790	7.440	4.870	1.650	1.420
14.080	5.600	8.470	6.390	1.940	1.870
LP2–LENG	LP2–WIDT	LM1–LENG	LM1–TA–W	LM3–LENG	LM3–TA–W
16	16	16	17	15	16
1.411	1.399	2.693	1.993	2.593	1.799
0.113	0.122	0.085	0.170	0.097	0.115
1.230	1.120	2.570	1.670	2.380	1.630
1.580	1.570	2.900	2.360	2.730	1.980
INTERO–W	NAKNOB–W	NAKNOB–H			
16	16	16			
3.008	8.709	6.148			
0.250	0.312	0.341			
2.430	7.880	5.480			
3.400	9.190	7.050			

Table 3. Combined basic statistical data of *R. l. foetidus* and *R. l. morio*, total observations: 8

	C–CONDYL	TOTAL–LE	BASIL–LE	ZYG–WIDT	MAST–WID
N. OF CASES	5	7	4	7	7
MEAN	26.346	29.483	19.950	15.014	13.186
STD DEV.	0.633	0.713	0.665	0.549	0.359
MINIMUM	25.320	28.050	19.140	14.490	12.680
MAXIMUM	26.960	30.230	20.710	16.080	13.800

C–C–WIDT	M3–M3–WI	UC–M3–LE	PALBRI–L	COCH–DIS	BRCASE–W
7	7	8	7	5	7
8.094	10.859	11.444	4.104	0.838	11.663
0.221	0.197	0.268	0.512	0.252	0.323
7.670	10.560	10.950	3.320	0.470	11.150
8.360	11.080	11.830	4.820	1.150	12.000

BRCASE–H	LACFOR–W	UC–P4–LE	UM1–M3–L	UC–BLENG	UC–WIDTH
5	7	8	8	8	8
8.336	6.174	5.189	6.721	2.511	2.190
0.302	0.326	0.091	0.036	0.014	0.020
7.840	5.570	4.780	6.400	2.250	1.980
8.650	6.480	5.740	7.000	2.630	2.380

UM1–LENG	UM1–WIDT	UP2–LENG	UP2–WIDT	BULLA–LE	MAND–LEN
8	8	8	8	6	8
2.570	3.054	0.791	0.926	4.502	20.875
0.037	0.052	0.013	0.092	0.240	0.378
2.360	2.660	0.610	0.790	4.140	20.040
2.880	3.400	0.950	1.040	4.760	21.310

LC–M3–LE	LC–P4–LE	LM1–M3–L	PR–COR–H	LP4–LENG	LP4–WIDT
8	8	8	8	8	8
12.283	4.780	7.561	5.434	1.680	1.635
0.238	0.222	0.169	0.106	0.096	0.116
11.890	4.490	7.220	5.310	1.560	1.470
12.580	5.040	7.730	5.580	1.820	1.790

LP2–LENG	LP2–WIDT	LM1–LENG	LM1–TA–W	LM3–LENG	LM3–TA–W
8	8	8	8	8	8
1.316	1.370	2.544	1.941	2.453	1.820
0.130	0.102	0.050	0.051	0.103	0.073
1.200	1.180	2.450	1.870	2.300	1.680
1.640	1.490	2.590	2.000	2.580	1.890

INTERO–W	NAKNOB–W	NAKNOB–H
8	7	7
2.580	7.814	5.816
0.234	0.379	0.332
2.320	7.320	5.280
3.040	8.400	6.340

In the following 18 characters *R. beddomei* appears to be significantly different from the rest of the material: C–CONDYL$^+$, TOTAL–LE$^+$, BASIL–LE$^+$, ZYG–WIDT$^+$, MAST–WID$^+$, M3–M3–WI$^+$, C–C–WIDT$^+$, UC–M3–LE$^+$, UM1–M3–L$^+$, UC–BLENG$^+$, UC–WIDTH, UP2–WIDT, MAND–LEN$^+$, LC–M3–LE$^+$, LC–P4–LE$^+$, LM1–M3–L, PR–COR–H$^+$, LM1–LENG$^+$. There are no overlaps in boxes made by the high-low graphs (Figs 12, 13) between the maximum values of *R. beddomei* and the minimum values of the other forms (for the small samples of *R. l. morio*, *R. l. foetidus*, and *R. beddomei* the actual minimum

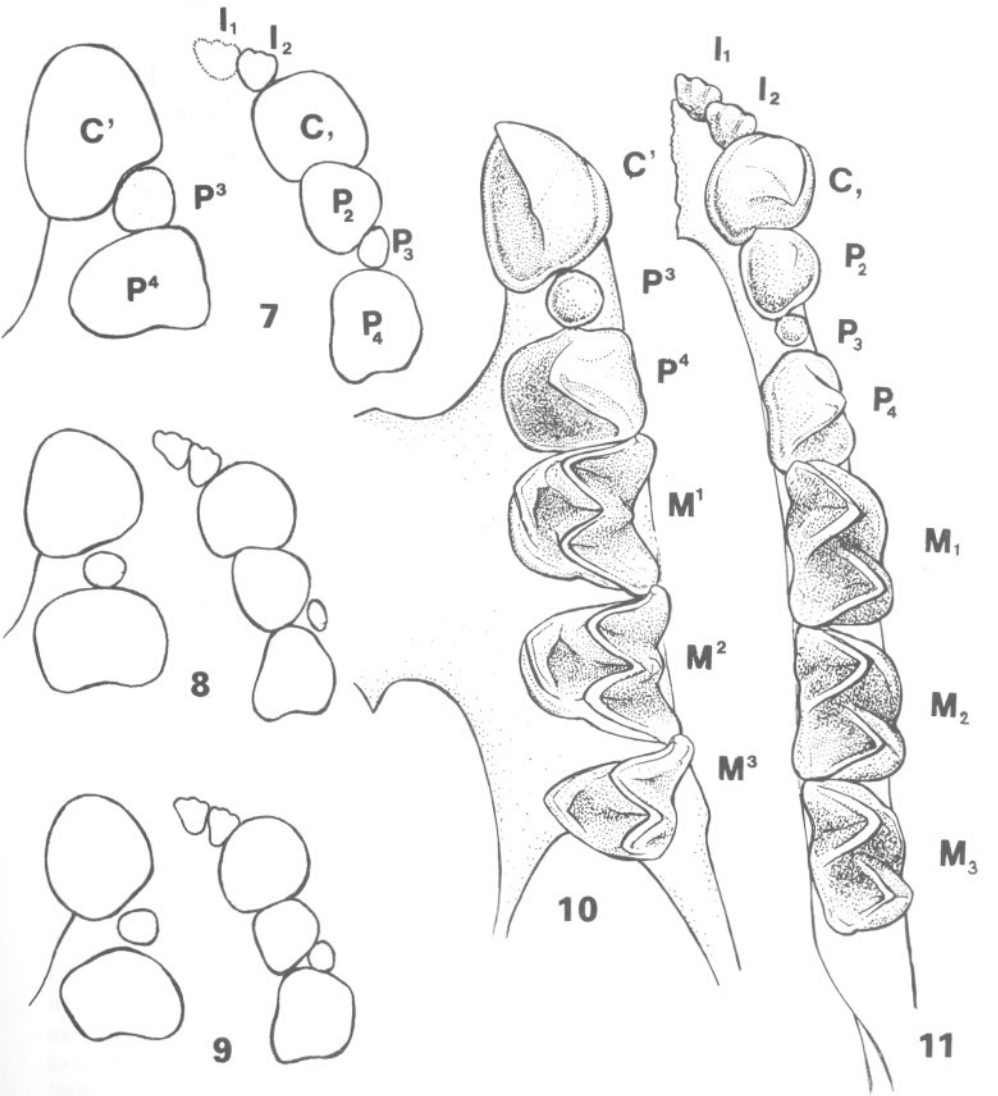

Fig. 7. Occlusal view of anterior part of upper and lower dentition in BNHM 92.2.7.3. *R. l. foetidus*
Figs 8-9. Occlusal view of anterior part of upper and lower dentition in *R. beddomei*, 8 = BNHM 12.11.28.5., 9 = BNHM 11.3.16.1.
Figs 10-11. Part of maxilla and occlusal view of upper dentition (Fig. 10) and part of mandible and occlusal view of lower dentition (Fig.11) in HNHM 11111 *R. l. perniger*

and maximum values, for the relatively greater sample of *R. l. perniger* the mean + and - standard deviation were used). In um1–leng and naknob–w^+ there are no overlaps, however the maxima of *R. beddomei* and minimum values of other samples are in contact.

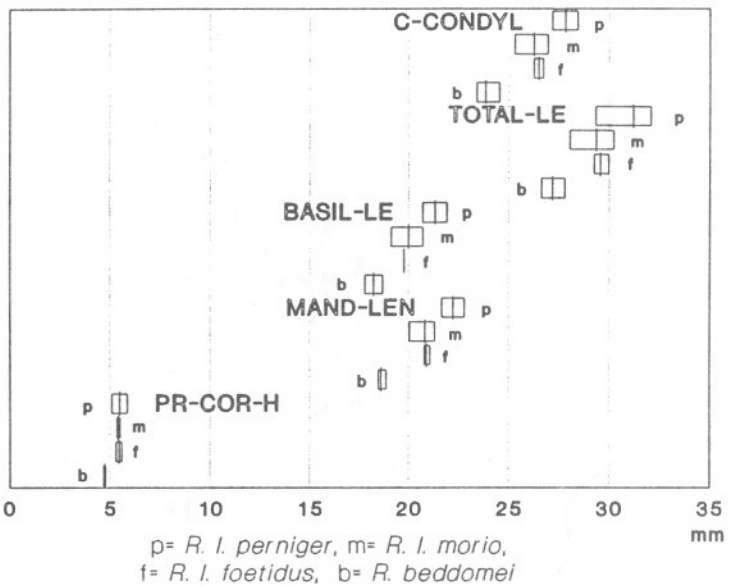

Fig. 12. High-low diagram for C–CONDYL, TOTAL–LE, BASIL–LE, MAND–LEN and PR–COR–H of *R. l. perniger*, *R. l. morio*, *R. l. foetidus* and *R. beddomei*

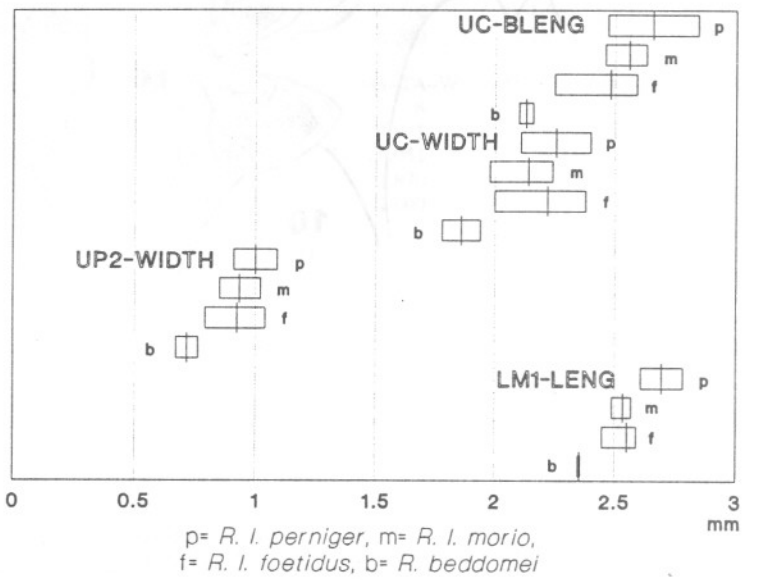

Fig. 13. High-low diagram for UC–BLENG, UC–WIDTH, UP2–WIDT and LM1–LENG of *R. l. perniger*, *R. l. morio*, *R. l. foetidus* and *R. beddomei*

For 15 variables marked with "+" (see above) further graphs (notched boxplots) showed the material of *R. beddomei* medians to be significantly different from all the others. An example is shown in Fig 14. (In the boxplots the horizontal

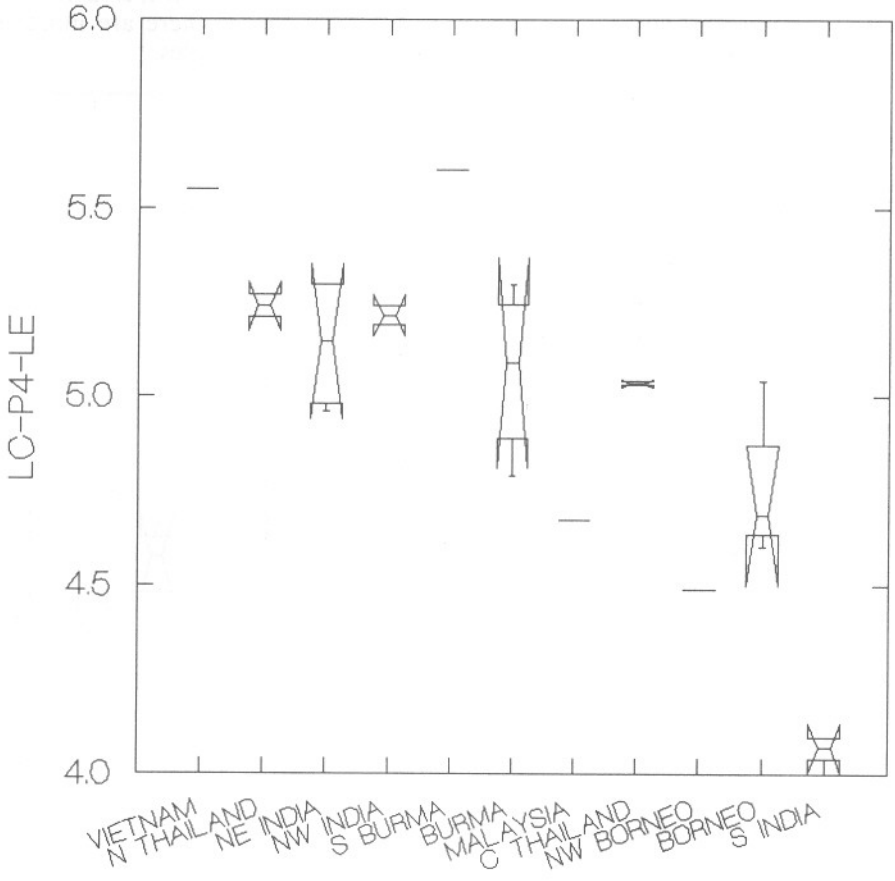

Fig. 14. Notched boxplot of lower C-P4 length in *R. luctus* and *R. beddomei*, grouped by localities

line represents the range of the sample, with vertical mark in the box as the median, the upper and lower margins (hinges) of boxes representing the interquartile range or midrange. Values outside the inner fences are plotted automatically with asterisks by the computer programme for some specimens slightly falling out of the sample, outside the outer fences with empty circles for strongly outstanding specimens. The boxes are notched at the median and return to full width at the lower and upper confidence interval values. Some of the outer confidence limits extend beyond the midrange. If the intervals around two medians do not overlap, one can be onfident that the two population medians are different [Wilkinson 1990]). In LP2–WIDT *R. beddomei* has overlaps with the Burmese and NE Indian (including Sikkim and Nepal) samples, while UC–WIDT, UP2–WIDT, LM1–M3–L and LM3–LENG of *R. beddomei* mostly overlap with the sample from C. Thailand, and LACFOR–W and UC–P4–LE with that of Malaysian

specimen, moreover, with the Bornean sample in BULLA–LE, UCP4–LE LP4–LENG and INTERO–WI. Only the example of UC–P4–LE is depicted here (Fig. 15). In all the other 13 measurements (PALBRI–L, COCH–DIS, BRCASE–H, BRCASE–W, UM1–LENG, UM1–WIDT, UP2–LENG, LP4–WIDT, LP2–LENG, LM1–TA–W, LM3–LENG, LM3–TA–W and NAKNOB–H) there are more or less extensive overlaps with the measurements of the other samples.

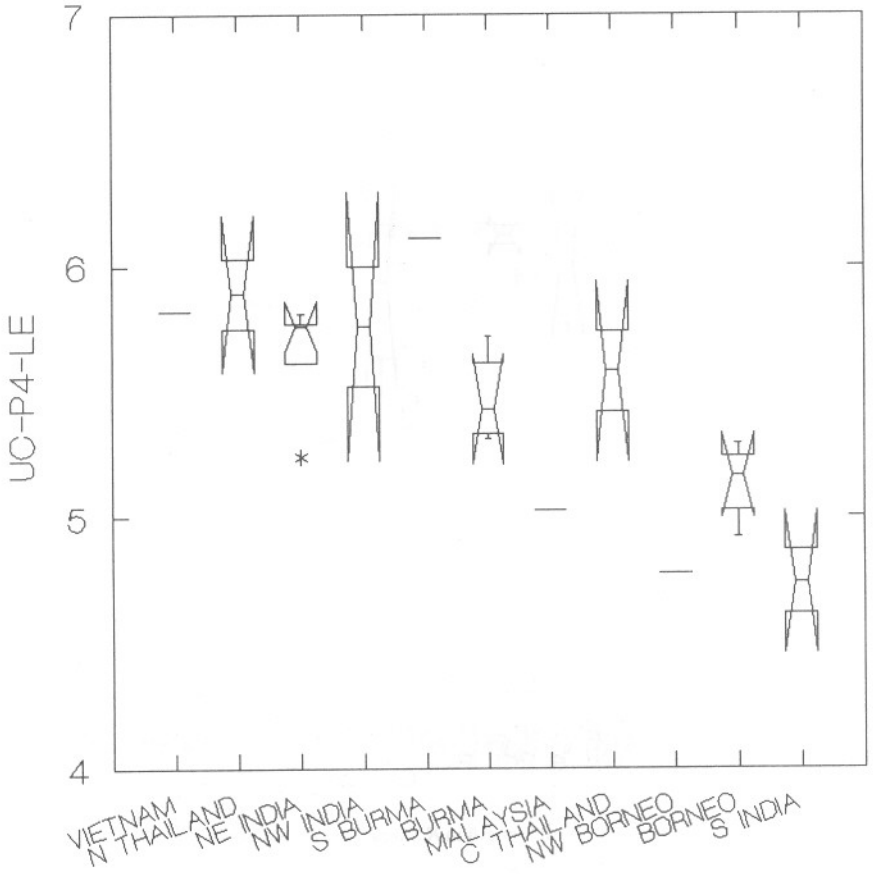

Fig. 15. Notched boxplot of upper C-P4 length, legend as for Fig. 14

The deviation of *R. l. perniger* from the more or less smaller other forms seems to be significant (the same way as above) in the following characters: c–condyl, mand–len, lm1–leng, while *R. l. morio* and *R. l. foetidus* diverges but in Brcase–w and intero–w.

Numerous scatter diagrammes showed appreciable differences between *R. beddomei* and the rest of material studied. Two of them are presented in this paper (Figs 16, 17) (where the straight lines represent the respective linear regression for the samples, ellipses for the 50% probabilities for the bivariate cloude of points). In each scatter-diagramme, for the greater samples the equations of the linear regression are also given).

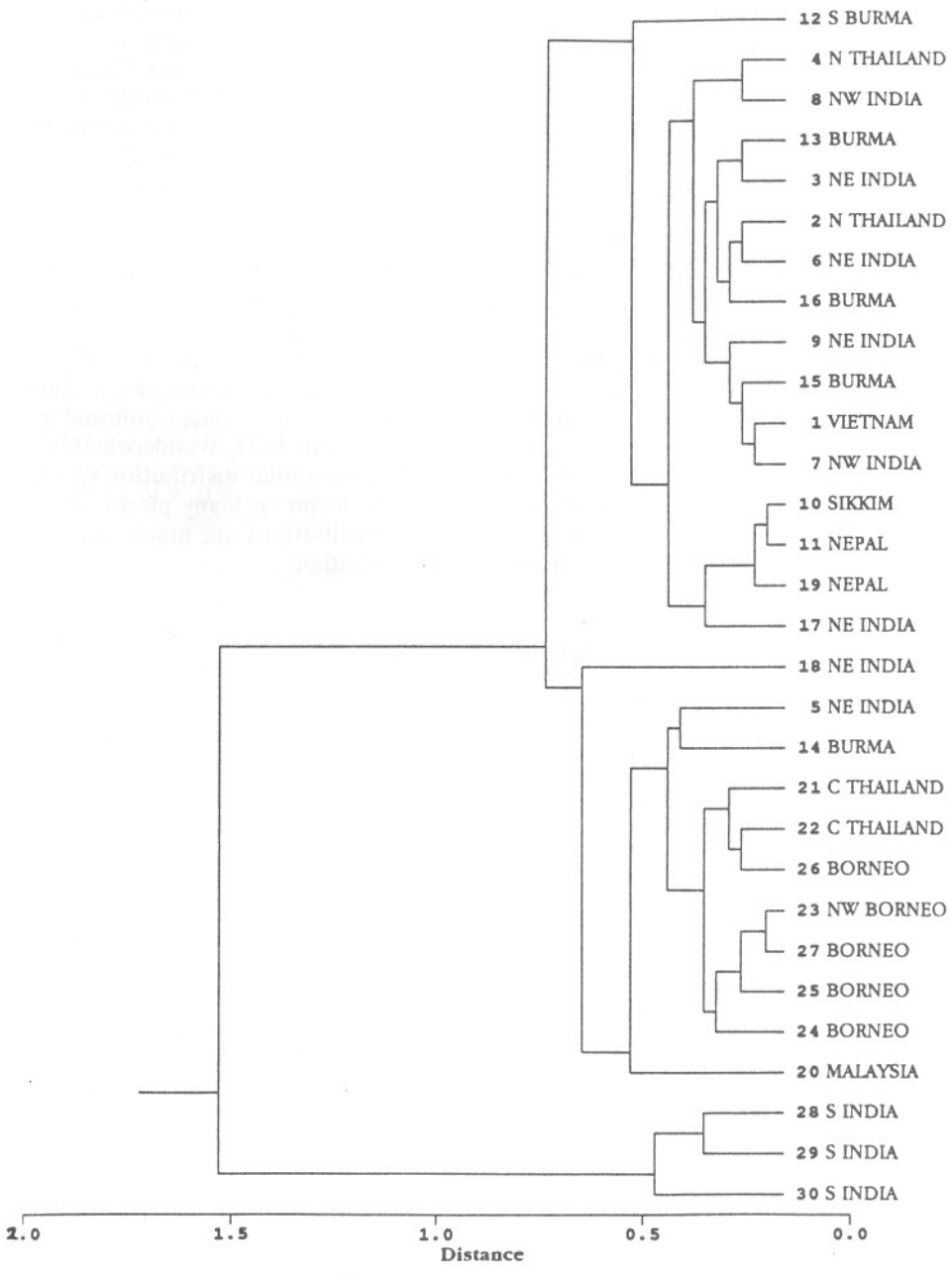

Fig. 18. Tree diagram made by the average linkage method for clustering *R. beddomei* and three subspecies of *R. luctus* (individual numbers see in the list of the material, other explanations in the text)

Conclusions

Though the present study material was limited, in light of the results it still seems reasonable to separate *R. beddomei* at specific level from the rest of the other subspecies of *R. luctus*. It has especially small size, relatively shorter lower and upper C-P4 rows, relatively longer upper and lower M1-M3 rows. Furthermore, it has narrower nasal portion, narrow C-C width, reduced width of P^2. Other cranial and dental features in some cases present probable convergencies with the smaller southern subspecies of *R. luctus*). Besides, the fact that *R. beddomei* has the farthest distributional area certainly not connected to those of the other similarily sedentary related forms, all support this assessment. The large gap between the distribution of *R. beddomei* and that of *R. luctus* is due to the great distance and the lack of suitable habitats in the Indian Peninsula between the Western Ghats and foothills of the Himalayas. One may suspect besides a probably rather recent connection during the last cool period of the Pleistocene (Mayr 1942) also other contacts and disjunctions between the southwestern and northern areas even during the earlier cool epochs. [There are examples of allopatric species for these areas among birds (e.g. Gallidae, Psittacidae, Capitonidae, Cuculidae, Columbidae, Corvidae and Timaliidae, see Ali 1977, Woodcock 1980) and even mammals (*Hemitragus*, see Prater 1965) with similar distribution in the Indian Subcontinent]. The various subspecies of *R. luctus* in many places intergade or at least the existing gaps between their distributions are much smaller. Actually, they show much greater similarities to each other.

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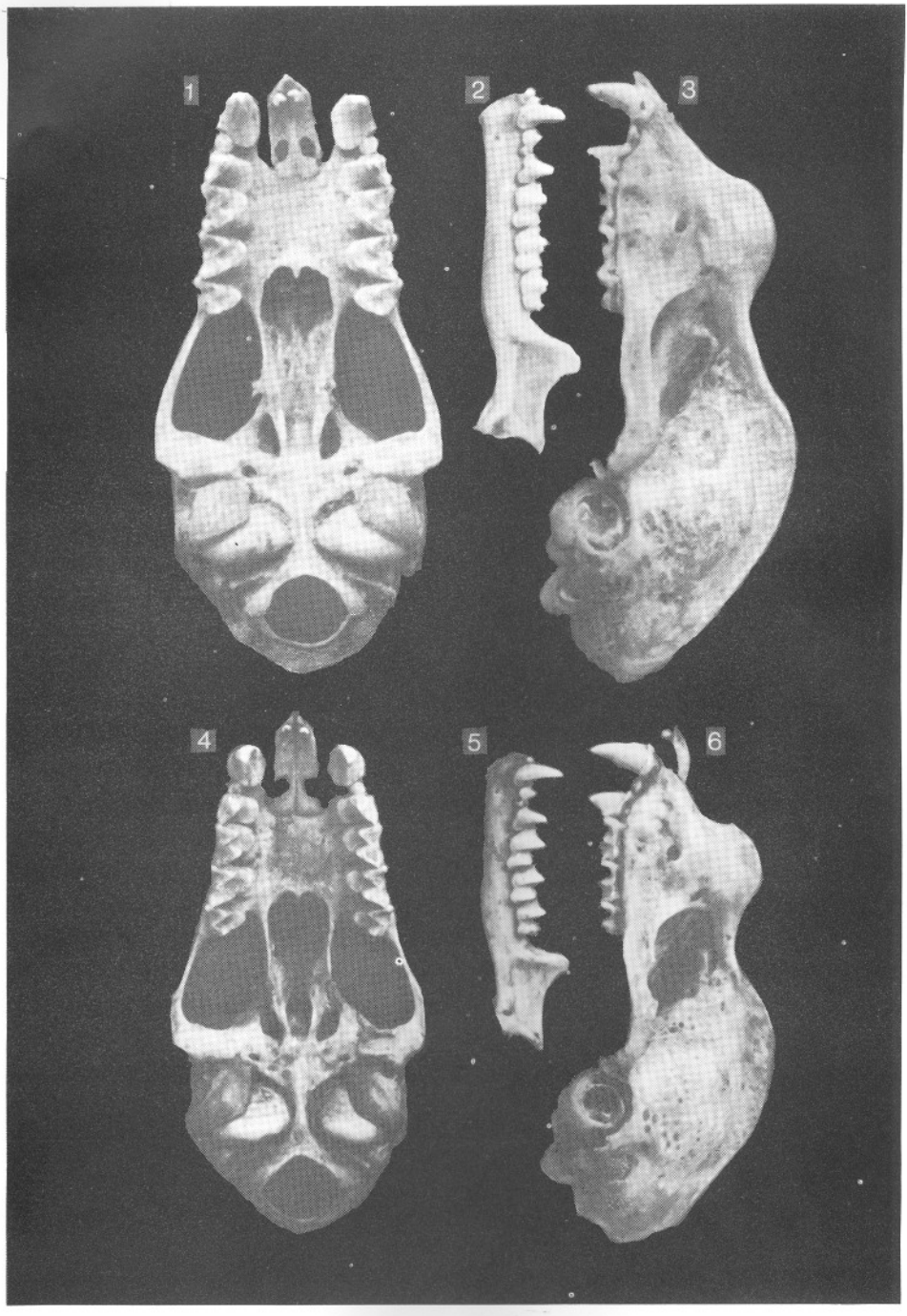

Figs 1, 3. Skull of the BNHS 3073 *R. l. perniger*; 1 = occlusal view, 3 = lateral view
Fig. 2. Labial view of mandible of BNHS 3073 *R. l. perniger*
Figs 4, 6. Skull of the BNHS 3081 *R. beddomei*; 4 = occlusal view, 6 = lateral view
Fig. 5. Labial view of mandible of BNHS 3081 *R.beddomei*