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REVIEW OF TAXONOMIC CHARACTERS IN AFRICAN BUZZARDS (GENUS BUTEO)

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ABSTRACT

This paper reviews various external characters in Old World buzzards (genus Buteo) in an attempt to clarify the taxonomic status of the small African Buteos. The results of shared characters indicate that B. trizonatus and B. brachypterus are closely similar and show resemblence to the japonicus-group of B. buteo which implies relict populations in southern Africa and Madagascar. Buteo oreophilus of eastern Africa is correlated in structure and some random aspects of plumage with B. auguralis and thus may be considered monophyletically related. On the great plumage disparaties and few character similarities B. oreophilus and trizonatus possibly should not be considered conspecific, pending further studies on apparent intermediates occurring in Malaŵi. At very least these forms are a superspecies.

INTRODUCTION

Four resident species of buzzards are currently recognized in the Afrotropical region including Madagascar (Stresemann & Amadon 1979; Brown *et al.*, 1982). These African buteos fall into three groups, all of which still present taxonomic problems.

One group includes the Mountain Buzzard B. o. oreophilus, B. o. trizonatus, and the Madagascar Buzzard B. brachybterus. They are all considered to be related to the Palearctic Buteo buteo of which one subspecies, vulpinus commonly reaches South Africa on migration. Which of these African buteos should be considered species remains debatable. The Mountain Buzzard is distributed in isolated populations in montane environments of eastern Africa; the range is disjunct with a southern subspecies *trizonatus*. Most probably the populations of the Mountain Buzzard from southern Tanzania (Turner, 1980; Stuart & Turner, 1980) and Malaŵi, Nyika Plateau (Dowsett & Dowsett-Lemaire, 1979) and Misuku Hills, belong to *oreophilus* (R. J. Dowsett in *litt.*), but no specimens were available for comparison.

Another group, the Jackal Buzzard *B.* rufofuscus is polytypic and aberrant in external characters from the Palearctic and other Afrotropical species. This group may form two species, wherein the southern race rufofuscus is separated from the two northern races augur and archeri (Brooke, 1975; Brown et al., 1982; Kemp, 1980). Unlike the Mountain Buzzard group, there seems to be no clearly related northern group. If any, one would be likely to hypothesize a link between *B. rufofuscus* and the Palearctic *B. rufinus*.

The Red-necked Buzzard *B. auguralis* is found in west to central Africa and is parapatric with *B. oreophilus* (Ituri and northern Kivu). It is similar in plumage pattern to *B. r. augur* and thus often considered as closely related to it (Smeenk, 1974). This is implied in species lists (Brown & Amadon, 1968; Stresemann & Amadon, 1979; Brown *et al.*, 1982). Snow & Smeenk (1978) point out that this may not be the case, and Siegfried (1970) suggests it is closely related to *B. oreophilus*. Whether the affinities are more to the Mountain Buzzard or the Augur Buzzard remains to be settled.

The Palearctic Buteo buteo falls into three groups (Vaurie, 1961): buteo-group in western Europe, including peripheral subspecies; vulpinus-group, eastern subspecies spending the non-breeding season in Africa; and the japonicus-group, containing four or possibly five members: japonicus, Japan; toyoshimai, Bonin Islands; oshiro, Daito Islands; refectus, Himalaya (Voous & Bijleveld, 1964); and populations resembling japonicus, Asian continent, which are larger than in Japanese birds (Momiyama, 1927; own data).

The systematics of these species have been discussed on many occasions; nevertheless, certain major taxonomic questions remain unsettled. The understanding of the relationships is confused by the wide variation in characters and inadequate diagnoses. Some current studies have been based on extrinsic characters, such as similarities in discontinuous distributions along African mountain ranges (Snow, 1978), and others on one or a few characters; proportions (Vaurie, 1961), and plumage pattern (Siegfried & Frost, 1973). This contribution evaluates various diagnostic characters and their taxonomic (value and tries to form a consensus on: 1) the relationship between oreophilus, trizonatus, and brachypterus and their affinities to B. buteo; 2) B. auguralis; and 3) finally to discuss some biogeographical implications.

In this study 1021 specimens were examined from the following museums: British Museum (Natural History), Tring, England; California Academy of Sciences, San Francisco, U.S.A.; Transvaal Museum, Pretoria; City Museum & Art Gallery, Durban, South Africa; Koninklijk Museum voor Midden-Africa, Tervuren, Belgium; Institute Royal des Sciences Naturelles de Belgique Brussels, Belgium; Rijksmuseum van Natuurlijke Historie, Leiden, Holland; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, W. Germany; Zoölogisch Museum, Amsterdam, Holland.

Statistical procedures included single factor analysis of variance and Student-Newman-Keuls (SNK) multiple range test, and Discriminant Function Analysis, stepwise procedure. Subroutines were run using the Statistical Package for the Social Sciences (Nie *et al.*, 1975) available through SARA, Amsterdam. Proportions were analysed after arcsine transformation of original data (Zar, 1974).

In general, methods in examination of specimens follow Baldwin *et al.* (1931), but for details see James (1984). Recently the name *B. tachardus* has been used for the Mountain Buzzard, however the long standing name *B. oreophilus* should be maintained (James & Wattel, 1983).

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RESULTS

Plumage pattern

Since there seems to be some confusion about the extent of the difference in plumage between B. o. oreophilus and B. o. trizonatus, I shall outline the differences which I find very striking. Rudebeck (1957; 1958; 1963; 1976) states that there is considerable difference in plumage; offers a detailed description of trizonatus, then compares some of its characters with nominate oreophilus (1957). On the other hand, Siegfried & Frost (1973) believe the differences are not as great, and those that do occur are in accordance with "Gloger's rule". However, without even considering the concentrations of melanins (Gloger's rule), the variation in feather and plumage patterning is great between the two groups.

Unlike the great individual variation of Buteo buteo, in nominate oreophilus the plumage pattern is stable. Adults from Rwanda and Burundi are very dark, almost black in pattern colour on a white ground; in ventral view they appear heavily marked black and white. The underside is seemingly blotched throughout with no clear margin between the breast and belly. Specimens from the Western Kivu Range and Rift Valley are similar but they are less strongly marked and have a cinnamon wash throughout. The tail colour is also a lighter brown. From slides of the type specimen AMNH 534546 collected in Ethiopia, a cinnamon wash is apparent on the underside. In discussing the back and scapulars, Rudebeck (1957) mentioned that only three of the five specimens he had available for comparison had a rufous admixture.

The plumage pattern shows greater individual variation in *trizonatus*. It is lighter overall than nominate *oreophilus* and shows a three zoned ventral pattern; the tail is lighter and washed tawny in colour and the tail banding is reduced; in *oreophilus* the dark bands are wide. The chin and under tail-coverts are usually unmarked, whereas in *oreophilus* they are always heavily marked.

According to Siegfried (1970), Frost & Siegfried (1970), and Siegfried & Frost (1973) adult and immature are indistinguishable, but the plumage is not completely the same. This holds true in both forms. In nominate *oreophilus* age was determined by wear and moult of primaries (*cf.* Brooke, 1974; Piechocki, 1963). This method proved more reliable than width of the subter-

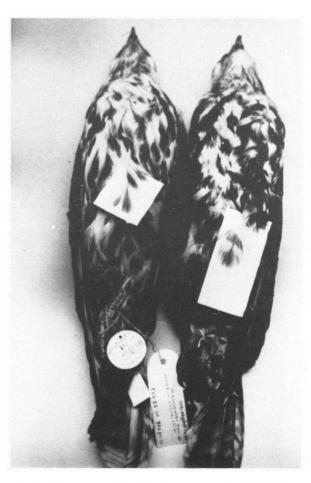


Fig. 1. Buteo o. oreophilus: Feather pattern in adult (right) and immature (left). Adults show horizontally marked patterns and immatures tear-shaped markings.

minal band on the tail, which is not very different in adult and immature. The underside is blotched in both age groups but the feather pattern in immatures is droplet shaped giving a more streaked pattern. The adult feather pattern is of incomplete bars and horizontally developed blotches (Figure 1). In *trizonatus* the lower belly in the adult is also more horizontally marked.

The three-zoned patterning of the ventral body plumage characteristic for trizonatus, is also found in B. brachypterus and B. b. japonicus. The latter is considered the Asian representative of B. buteo, and is grouped with associated island populations under the general name japonicus-group by Vaurie (1961). The subspecies japonicus can be described as a subgroup of B. buteo characterized by streaked rather than barred underside, no or faint tail bars and more extensively feathered tarsus (Kuroda, N. H. & M. Morioka, 1974; own data). Characteristically, both immature and adult plumages are streaked, although the adult plumage is more horizontally marked on the lower belly. Not only is the underside "trizoned", similar to trizonatus; viz., broadly streaked breast, cream or cinnamon-cream upper belly and a marked lower belly, but the size of B. b. toyoshimai is small, almost equalling trizonatus. From mainland Asia a small percentage of japonicus exhibit barring on the lower belly while some are totally dark.

Ground Colour

The ground colour of the underside is white with some buff wash in *oreophilus* and *auguralis*, whereas in *trizonatus*, *brachypterus*, and the *japonicus* group it is cream or cinnamon-cream.

Under tail-coverts

The under tail-coverts are characteristic to each group. They are white, marked with dark in both adult and immature nominate *oreophilus*, white to cinnamon white, unmarked in *auguralis*, cinnamon-cream and unmarked in both adult and immature *trizonatus* and *japonicus*. In *B. brachypterus* the adult under tail-coverts are unmarked cinnamon-cream in colour, but in the immature they are marked with broad streaks.

Primary tip banding

The tips of the primaries are usually dark in the Palearctic species, but in the Afrotropical ones some show white banding up to the tip. In almost all cases *B. brachypterus* is clearly banded to the tip of primaries. Of 23 skins, where primary tip banding was recorded in nominate *oreophilus*, 12 were banded to moderately banded. These were mainly adults from the Kivu area. The remaining 11 included both immatures and adults from eastern Africa. *B. o. trizonatus* shows much less banding and *auguralis* is only slightly banded in few individuals. All of the four specimens examined from the Bonin Islands (*toyoshimai*) showed banding to primary tip. However, most of the *japonicus* group do not show banding.

Tarsal feathering

Difference in length of the feathered portion of the tarsus was mentioned by Chapin (1932) and Rudebeck (1957) for different populations of B. oreophilus, the latter thought it to be a very good character. Chapin (1932) reported that the front of the metatarsus was bare for only 35 mm, though, as Rudebeck (1957: 427) points out he probably measured from the tip of the longest feather in front and not from the insertion of the lowest feather as suggested in Baldwin et al. (1931). My measurements are similar for the trizonatus specimens measured by Rudebeck (1957: Table 1 & 2) except for tarsus and unfeathered portion of tarsus. His bare portion averages are 38.3 mm for trizonatus, and 41.2 mm for oreophilus, whereas my average for the same trizonatus specimens (except two) is 34.0 mm. Calculating the percentage of tarsus feathered I arrived at 43% trizonatus, 36% oreophilus from Rudebeck's data, and from my data at 49.5%, 43.6% respectively, and 58.3% in japonicus. For a general rule of thumb, the feathered portion in oreophilus and auguralis are less than 50%, brachypterus and trizonatus greater than or equal to 49% and japonicus greater than 50% of tarsus length (Figure 2).

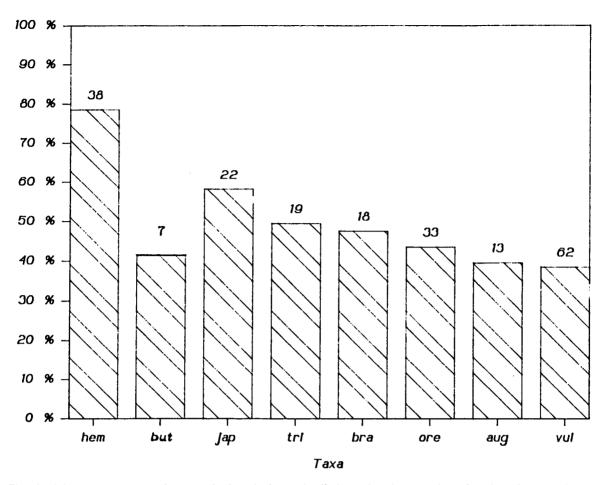


Fig. 2. Histogram-Percent of tarsus feathered. hem = hemilasius, tri = trizonatus, jap = japonicus, bra = brachypterus, ore = oreophilus, vul = vulpinus, aug = auguralis, but = buteo.

Tail pattern

Rudebeck (1957) gives a detailed description of the tail pattern in *trizonatus*. In general, the adult tail pattern can be categorized into two types. One is rufous-brown with hints of dark bands and one clear dark subterminal band. One subadult specimen (BM1905.12.29.114) I examined, showed a worn immature tail, heavily banded (7 to 9 dark bands) except for one freshly emerged central retrix. This new feather had a pattern of the above mentioned type. The other category is one having a wide subterminal band and numerous other bands. However, many specimens show a wide variation falling between the two categories. The tail pattern in the *japonicus*-group is strikingly similar. The pattern in oreophilus does not show this variation and is usually olive-brown to lighter brown with a blue black subterminal and 6-7 black bands. The width of the bands is about equal to the lighter areas between the bands, whereas in trizonatus the bands, when present, are fewer and slightly narrower. In auguralis, adults have a tawny rufous tail with one subterminal dark band; and immatures have many more bands. However, some obscure banding may persist in older birds. The base of the rectrices is white. In brachypterus the tail base is also white in adults but not in immatures. Immatures differ from adults in (1) lack of white at base of tail, (2) more dark tail bands, and (3) under tail-coverts are broadly streaked where in adults they are unmarked cream or cinnamon cream.

Table I. Leg and cere colour in Old World Buteo. Colours are from specimens labels, except in *trizonatus* which are reported by Palmer *et al.* (1985).

	leg	cere				
buteo	yellow	yellow				
vulpinus	yellow	yellow				
oreophilus	yellow	yellow				
auguralis	yellow	yellow				
trizonatus	pale yellow green	pale yellow green				
brachypterus	greenish yellow	greenish yellow				
japonicus-group	greenish yellow	greenish yellow				
hemilasius	greenish yellow	greenish yellow				
rufinus	yellow	yellow				
rufofuscus	yellow	yellow				

Colour of bare parts

The colour of the bare parts is sometimes important at lower levels in taxonomy. In the genus Buteo there is no indication that leg, feet and cere colour vary greatly between age, sex or breeding condition. The Old World species have either yellow or greenish yellow legs and cere. Browsing through colours reported in Brown & Amadon (1968), this seems also to hold true for the New World species. If leg and cere colour is a useful character or how reliable it is, is difficult to say. However, there seems to be some pattern in the occurrence of greenish yellow legs in relation to other characters. In Old World groups those with tri-zoned, or nearly so, plumage pattern have greenish yellow legs and strongly feathered tarsi. Table I lists cere and leg colours. In addition, those New World species which have either leg or cere, or both greenish yellow are B. lineatus, B. solitarius, and as well as all species with three emarginated primaries (except B. galapagoensis).

Structure

In table II some ratios are set out, in part because Vaurie (1961) separated *oreophilus* from B. *buteo* on proportion of tail and wing. Siegfried & Frost (1973) also calculated tail-wing ratios finding no differences between *oreophilus* and *vulpinus*, which occurs as a migrant in South Africa.

The results from oneway analysis of variances indicate that the tail-wing ratios of the small African buzzards are not significantly different from *vulpinus*. However, they are significantly different from nominate *buteo*. This ratio is not a very good taxonomic character judging from the difference between nominate *buteo* and *vulpinus* which are without much doubt conspecific. The Steppe Buzzard is a long-distance migrant and this expectedly affects the length of tail and wing. But why the proportions of the resident Africa forms should agree with the highly migratory *vulpinus* is unclear.

The actual culmen length in *trizonatus* (males $\overline{X} = 20.2$; n = 8, females $\overline{X} = 22.0$; n = 9) and nominate *oreophilus* (males X = 21.1; n = 24, females $\overline{X} = 22.9$; n = 26) are similar to those of *vulpinus* (males $\overline{X} = 20.4$; n = 61, females $\overline{X} = 21.8$; n = 59). The relationship between culmen and wing lengths for all groups are depicted in a scattergram (Figure 4), along with calculated least square regressions.

There is a similar linear continuum for data points in *vulpinus* and nominate *buteo*. Their correlation coefficients are not significantly different (Z = 1.91 > 1.96; P < .05). Data points plotted for *vulpinus* are those from specimens collected in the Afrotropical Region, but in calculating the correlation coefficient and LS regression, Palearctic specimens were included. There is essentially no overlap between *vulpinus* and *oreophilustrizonatus*. Another point is the similarity and overlap in the distribution of data points in *oreophilus* and *auguralis*.

I compared all the correlation coefficients and find they are not significantly different ($\chi^2 = 0.76$; P < .05), with one exception: for *trizonatus* (Z = 0.35 < 1.96; P < .05).

Discriminant Function Analysis

The aim in this procedure is limited to the separation by size and structure only of groups chosen a priori. Ratios are purposely omitted from the analysis because conclusions can be biased depending upon the correlation of the numerator and denominator, the ratio is not necessarily independent of the numerator and the use of ratios alters the factor structure of the covariance matrix (Humphries *et al.*, 1981).

Table II. Oneway ANOVA for Tail/Wing and Culmen/Wing ratios in the Old World buzzards. Correction values (Arcine transformation) used in calculations of "f" values and homogenous subsets (SNK). Vertical lines indicate groups of homogenous subsets.

	Tail/Wing Ratio (%)					Culmen/Wing Ratio (%)					
Adult males Group	N	Mean	SD	Min	Max	Males Group	N	Mean	SD	Min	Max
rufofuscus	14	42.7	1.71	39.0	45.3	buteo	51	5.64	0.30	5.18	6.55
augur	24	43.9	1.37	40.9	45.6	vulpinus	60	5.65	0.21	5.16	6.15
auguralis	11	50.0	1.81	48.0	54.7	japonicus	20	5.87	0.30	5.39	6.38
trizonatus	6	50.4	0.98	49.1.	51.6	trizonatus	7	6.07	0.15	5.86	6.27
oreophilus	17	50.7	1.17	48.8	52.6) oreophilus	23	6.24	0.30	5.58	6.95
vulpinus	47	51.2	1.43	48.8	55.0	auguralis	16	6.27	0.23	5.83	6.67
brachypterus	15	53.2	0.96	51.7	55.7	rufofuscus	15	6.27	0.38	5.63	6.90
buteo	35	54.2	1.91	50.4	58.3	augur	24	6.30	0.31	5.68	7.10
japonicus	13	54.9	1.53	52.1	57.5	brachypterus	22	7.45	0.46	6.71	8.58
F = 151.0;	P <	.000;	DF -	- 181			$\mathbf{F}=89.$	7;	P<.000;		DF = 23
Adult females						Females	<u>#_</u>				
Group	Ν	Mean	SD	Min	Max	Group	Ν	Mean	SD	Min	Max
rufofuscus	11	43.4	0.98	41.9	45.2	buteo	60	5.81	0.30	5.06	6.50
augur	12	44.5	3.71	40.5	51.5	vulpinus	58	5.85	0.24	5.38	6.52
oreophilus	17	50.1	1.08	47.4	51.9	japonicus	15	5.93	0.35	5.50	6.54
vulpinus	50	50.8	1.68	48.3	57.5	trizonatus	9	6.25	0.22	5.93	6.52
auguralis	13	51.2	2.72	47.8	57.8	oreophilus	26	6.39	0.18	5.96	6.82
trizonatus	4	51.8	2.19	49.0	54.1	rufofuscus	18	6.42	0.27	5.96	6.74
brachypterus	15	52.3	1.70	49.2	55.1	auguralis	17	6.43	0.17	6.09	6.74
buteo	36	53.7	1.21	51.3	56.2	augur	18	6.43	0.25	5.84	6.81
japonicus	14	55.0	1.98	51.1	58.0	brachypterus	21	7.45	0.26	6.57	7.74
F = 60.6; P < .0	000; D	F = 171				F = 94.0; P<	.000; D	F = 241.			

Figure 3 is a graphical representation of the different groups in relation to size. Tarsus length produced the greatest contribution to separation of the groups (Roa's V = 1968.6 alpha = .000) followed by wingtip. The classification phase of DFA procedure correctly classified only 77.8% of the 432 cases processed in the analysis. This is in fact a rather poor percentage, which means that many individuals were classified as belonging to another group. However, this also indicates that groups overlap in many morphometric characters, and since groups were chosen a priori, their group delimitations may not be well defined.

In Figure 3 three major clusters of groups are seen. All individuals of *brachypterus* were classified correctly. This is a unit apart. The abnormally long tarsus and culmen which are probably attributed to "island effect", and broad wingtip in comparison to its other characters help to separate it from the other groups. The Jackal Buzzard, *augur* and *rufofuscus*, is separated clearly from *auguralis* which is contained in a cluster including *trizonatus*, *oreophilus* and interestingly *toyoshimai*. The latter cluster is not clearly separable from the Palearctic groups.

Two important conclusions may be made from these data. In the first case, toyoshimai is closely similar in size to trizonatus, oreophilus, and auguralis. However, this group shows intimate affinities with japonicus which is not clearly apparent from Figure 3. This is probably due to the fact that individuals with a wing length shorter than 359 mm and only Japan as locality on the specimen label were identified as toyoshimai and consequent-

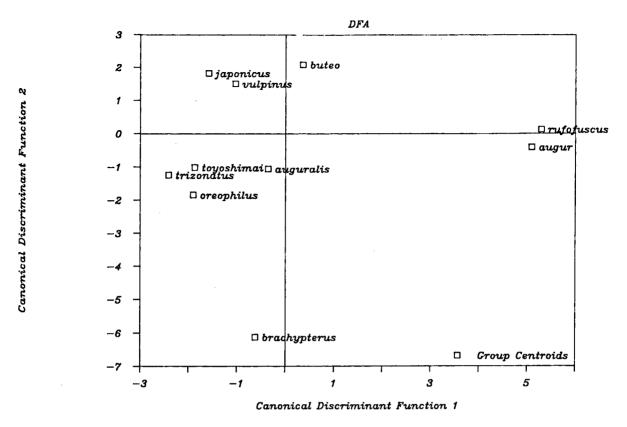


Fig. 3. Results of Discriminant Function Analysis: All group scatterplot-group centroids.

ly classified under that group. The second conclusion is that *auguralis* is closest in size, not to *B. augur*, but to the *oreophilus-trizonatus* group.

DISCUSSION

Siegfried (1970) and Siegfried & Frost (1973) grouped the small African *Buteos* by similarities in the "ontogenetic pattern system", a character used by Johnson & Peeters (1963) in classifying the "woodland hawks"). They distinguished two elements; one with similar adult and immature ventral body plumage, both vertically marked (*oreophilus* and *trizonatus*), and another barred in adult and streaked in the immature (*B. b. vulpinus*). Siegfried (1970) went further and proposed that the non-dimorphic age element is atavistic, although no concessions are made for parallelism or neoteny. This Haeckelian viewpoint is also the base assumption of Johnson & Peeters (1963), namely "that within a species the juvenal plumage is probably closer to the ancestral than is that of the adult." Amadon (1982) points out that the plumage similarities in the "woodland hawks" may be "superficial" and "ecological".

Leaving aside suppositions on the derived and non-derived state in the plumage characters, the taxa can be grouped by similar characters outlined herein. First, oreophilus and trizonatus are intrinsically forest dwellers, and show Accipiter-like flight behaviour (J. C. Sinclair pers. comm.). Even B. auguralis is known to nest in forests and inhabitat forest edges (Brown & Amadon, 1968, Bannerman, 1951), although it is better known as an open woodland savanna bird. B. o. oreophilus adheres closely to the montane forest zone, trizonatus to relict indigenous forests and plantations (Martin et al., 1981a, 1981b; Steyn, 1982; Siegfried, 1968) although usually nesting in ex-

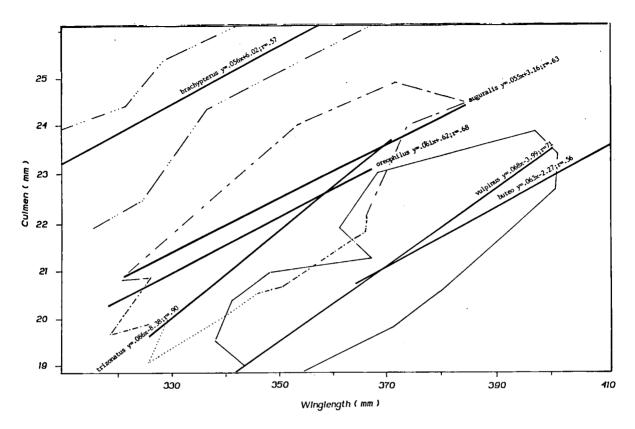


Fig. 4. Scattergram-Winglengths vs. Culmen.

otic pines (Palmer et al., 1985). B. brachypterus is variously reported to live in forests (Thiollay & Meyburg, 1981), forest edge (Steyn, 1982), and wooded and open country (Brown & Amadon, 1968). It is rather surprising that despite similar ecological restrictions and structure, certain character states such as plumage pattern vary between groups. Unlike the convergence of plumage pattern towards accipiters seen in the "woodland hawks", the forest taxa in the Afrotropical do not show clearly barred ventral pattern. Interestingly, the Western Palearctic buzzard, also a woodland bird, does.

The groups which share a three-zoned ventral plumage, (*japonicus*-group, *trizonatus* and *brachypterus*) also share an extensively feathered tarsus, cinnamon-cream wash, greenish yellow cere and legs, and some primary tip banding. Nominate *oreophilus* shows no clear separation of plumage zones, whereas the western Palearctic buteo and vulpinus characteristically have a light gap between the breast and belly. Rudebeck (1963) suggested that oreophilus may have retained a more primitive colour pattern. I have shown that at least feather patterns do vary in different ventral plumage zones. I feel it may show a more specialized plumage pattern for forest-life.

The characters of the components of the *B.* buteo group are interrelated in various ways suggesting close relationship. Thiollay & Meyburg (1981) reported *B. brachypterus* as strictly a forest bird with no equivalent in Africa and Asia. However, I present reasons which indicate that trizonatus of southern Africa is closely allied to brachypterus, and both are related to the Asian japonicus-group. Nominate oreophilus is greatly dissimilar in plumage details from trizonatus (Figure 5a & b), and although phylogenetically related to it, may be separated at a higher level than subspecies. At what level is not clear. If it were not for populations from Malaŵi and southern Tanzania which are not assigned to either subspecies and of which the descriptions are not documented, I would be inclined to consider *trizonatus* a separate species, or at least separable as an allospecies. Moreover, some specimens I have seen identified as *vulpinus* from the Nyika Plateau, Malaŵi, and in particular BM1932.2.25.567 collected in much the same habitat (C. W. Benson *in litt.*) as Dowsett & Dowsett-Lemaire (1979) observed the first *oreophilus*, show many intermediate characters. But these characters point more to *vulpinus* than *trizonatus*.

The Red-necked Buzzard B. auguralis shares many common characters with the smaller African buzzards and may belong with oreophilus under a monophyletic group. The adult plumage which is similar to B. r. augur, especially its red tail and white underparts, is surely a convergent character. Its structure is similar to oreophilus as is its immature plumage pattern. Hartert & Neumann (1914) initially identified specimens of oreophilus as immature auguralis. Siegfried (1970) mentions that auguralis is similar to oreophilus in underwing pattern, voice and tail-wing ratio. Results from DFA and Oneway ANOVA of ratios (Figure 4 and Table II) indicate that its structure does not differ greatly from oreophilus. Chapin (1932) noted the call of oreophilus as almost exactly like the Red-shouldered Hawk B. lineatus of North America and likewise B. b. buteo. Furthermore, he mentioned that the voice of B. auguralis is reminiscent to B. lineatus and B. b. buteo.

Vaurie (1961) separated *B. oreophilus* as a valid species from nominate *buteo* on proportional differences in tail-wing ratio. However, tail-wing ratio of *oreophilus* and *trizonatus* is not significantly different from *B. b. vulpinus* (Table II). Siegfried & Frost (1973) disputed Vaurie's calculations on statistical grounds and also found no statistical difference between *trizonatus*, *oreophilus*, and *vulpinus* (Student's t Test). The Steppe Buzzard seems a logical source for comparison because *vulpinus* is widespread in Africa during the Palearctic winter especially in southern Africa.

Taxonomy and Biogeography

Hartert & Neumann (1914) described *B. oreophilus* as a new species of buzzard from eastern Africa. It was subsequently reported from southern Africa by Sclater (1919), and Courtenay-Latimer (1941), the former author regarded it as the resident race of *B. buteo*. When Rudebeck (1957; 1958) formally described the southern population giving the name *trizonatus*, he reluctantly included *trizonatus* and nominate *oreophilus* under *B. buteo*, although he originally intended to place it under nominate *oreophilus* apart.

Whether B. oreophilus is a good species or not is still debatable. Meinertzhagen (1951), mainly on biogeographical grounds, considered B. oreophilus and B. brachypterus as the African representatives of the Palearctic Common Buzzard and thus recent colonists, a stand taken by many current authors (Broekhuysen, 1967; Snow 1978; Snow & Smeenk, 1978; Voous, 1960). Vaurie (1961) and Siegfried & Frost (1973) consider B. oreophilus a valid species. Presently, most follow Stresemann & Amadon (1979) who place them in a superspecies complex.

The results of shared characters as outlined here have indicated that *trizonatus* and *brachypterus* are closely similar and show resemblance to the *japonicus*-group. The biogeographical implication points to relict populations in southern Africa and Madagascar which stemmed from a *japonicus*-like ancestor. Nominate *oreophilus* may form a natural group with *auguralis* being as closely related to that species as it is to *trizonatus*. On account of the great differences in plumage and few relative character similarities, *oreophilus* and *trizonatus* do not seem to be conspecific.

Where the larger buzzard *B. rufofuscus* fits in is puzzling. It is increasingly evident that *B. rufofuscus* is specifically distinct from *B. augur* and *archeri* (Brooke, 1975; Brown, 1972; Brown, 1984; Brown *et al.*, 1982; Prigogine, 1984); differences being summarised by Brooke (1975). Further, both *rufofuscus* and *augur* are resident in Namibia (Kemp, 1980) and no intermediates are known. Siegfried (1970: 42) suggests that *B. rufofuscus* may be allied to some Palearctic stock represented by *B. rufinus*. There seems to be little ground for

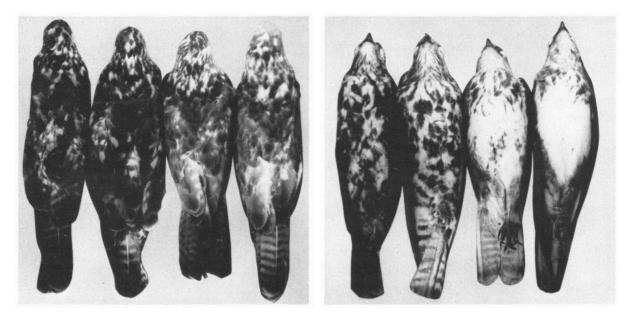


Fig. 5a and b. Buteo oreophilus: trizonatus (right two) and oreophilus (left two).

this other than possibly similarity in size which in itself does not necessarily indicate phylogenetic closeness. Neither the plumage pattern nor the flight of nominate *rufofuscus* resembles any other species in *Buteo* and *augur* only to a degree (Brooke, 1975), although I admit some resemblence of it to Neotropic *B. polysoma*. The full adult plumage is not acquired until two and half to three years (Friedmann, 1930; Brown *et al.*, 1982), the immature plumage is rather unlike any Palearctic juvenile form, and the structure and proportions are not similar to those of any African *Buteo*.

CONCLUSION

As I have shown the characters of the components of the *B. buteo* group are interrelated in various ways suggesting close relationship, though in some cases the character variation appears almost at random. For example similarity in plumage in *B. o. trizonatus* and *B. brachypterus* of Africa to the japonicus group of *buteo*, especially the Bonin Island race, and disparate leg feathering (similar in southern African groups to *japonicus*) and variation in proportions not showing a clear geographical pattern. If brachypterus and oreophilus are to be kept specifically distinct from buteo, which is to be strongly recommended, then from what I and others have shown trizonatus might be as well. It is perhaps hazardous to separate oreophilus and trizonatus as species, pending field studies. In any case all these forms at very least constitute a superspecies.

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