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THE EVOLUTION AND SYSTEMATICS OF THE PHOENICULIDAE

by N.C.Davidson

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INTRODUCTION

The problems inherent in elucidating the evolution and affinities of a uniform family such as the wood-hoopoes (Phoeniculidae) are great, and there has been considerable dissent about their taxonomy, one to three genera having been recognised. Geographical distribution as an indicator of affinity together with plumage, mensural, ecological and behavioural characters permit a reappraisal of the group using a wide range of information (Fry 1969). This paper is limited to an appraisal of affinities within the Phoeniculidae and does not attempt to relate its affinities within the Coraciiformes.

Localities have been taken from skins in the collection of the British Museum (Natural History), Tring, and abstracted from the literature. They have been point plotted in Figs. 3-5, allowing detailed examination of distribution patterns using the methods of Hall & Moreau (1970). Data on ecological and behavioural characters from the literature are considered in conjunction with geographical distribution where they appear relevant to systematics.

CHARACTERS

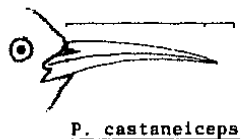
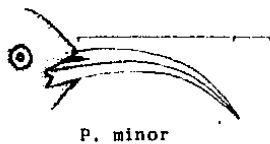
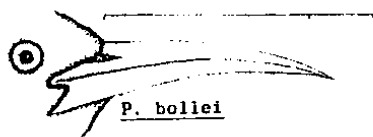
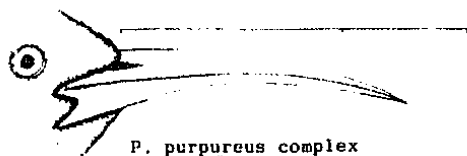
The taxa of wood-hoopoes recognised by White (1965), Peters (1945) and MacKworth-Praed & Grant (1957, 1962, 1970) are listed in Table 1. All wood-hoopoes inhabit wooded savannas except P. bollei and P. castaneiceps which are forest species.

Most accounts (e.g. Mackworth-Praed & Grant op. cit., Bannerman 1933, Bates 1930, Clancey 1964 and Roberts 1940) list three genera. The generic distinctions appear to have been overall size, bill morphology, and leg and foot colour (Fig. 1; Table 2). Phoeniculus comprises species with heavy, slightly decurved bills and red feet, whilst both Scopelus and Rhinopomastus are small with black legs and feet. The last two genera differ in bill shape, Scopelus with a short straight bill and Rhinopomastus long and greatly decurved (Fig. 1).

The monogeneric classification by White (1965) suggests greater uniformity and mostly follows Peters' (1945) scheme.

At subspecific level taxonomic characters are variation in iridescence, bill colour, presence or absence of white in wings and tail (Fig. 2) and measurements. Some subspecies are poorly defined and variability within widespread ones like P. p. marwizi is considerable.

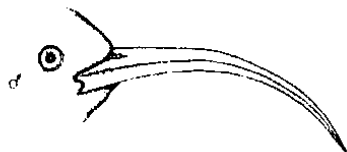
Juveniles of all species show greater similarity than do their adults, because of reduced iridescence and all-black bills.

a). ♂ Phoeniculus spp.

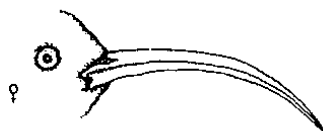
Scales indicate length ranges

b). Sexual dimorphism in P. cyanomelas

c. schalowi



c. cyanomelas



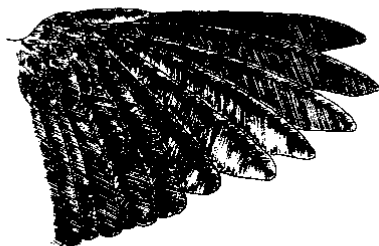
0 30mm

Figure 1. Bill morphology of the Phoeniculidae

Wing with white 1^o bar (e.g. purpureus
complex, aterrimus)



Wing wholly dark and glossy
(e.g. castaneiceps, bollei)



Tail long and graduated with white spots (e.g. purpureus complex,
some cyanomelas)



Tail long and graduated lacking white spots (e.g. castaneiceps,
bollei, minor)



Tail short and square (aterrimus)



(not to scale)

FIGURE 2. Plumage characters of the Phoeniculidae

THE *P. purpureus* COMPLEX :*P. purpureus*, *P. somaliensis*, *P. damarensis*. Fig. 3

These large forms live in a wide range of savanna habitats occupying the whole of sub-Saharan Africa except desert and forest. Their plumage is dark and is usually iridescent brassy green, duller and bluer in West Africa, and duller and more purple in Ethiopia and Somalia. The bill is red except in Mauretania and Ethiopia/Somalia where it is partly or wholly black.

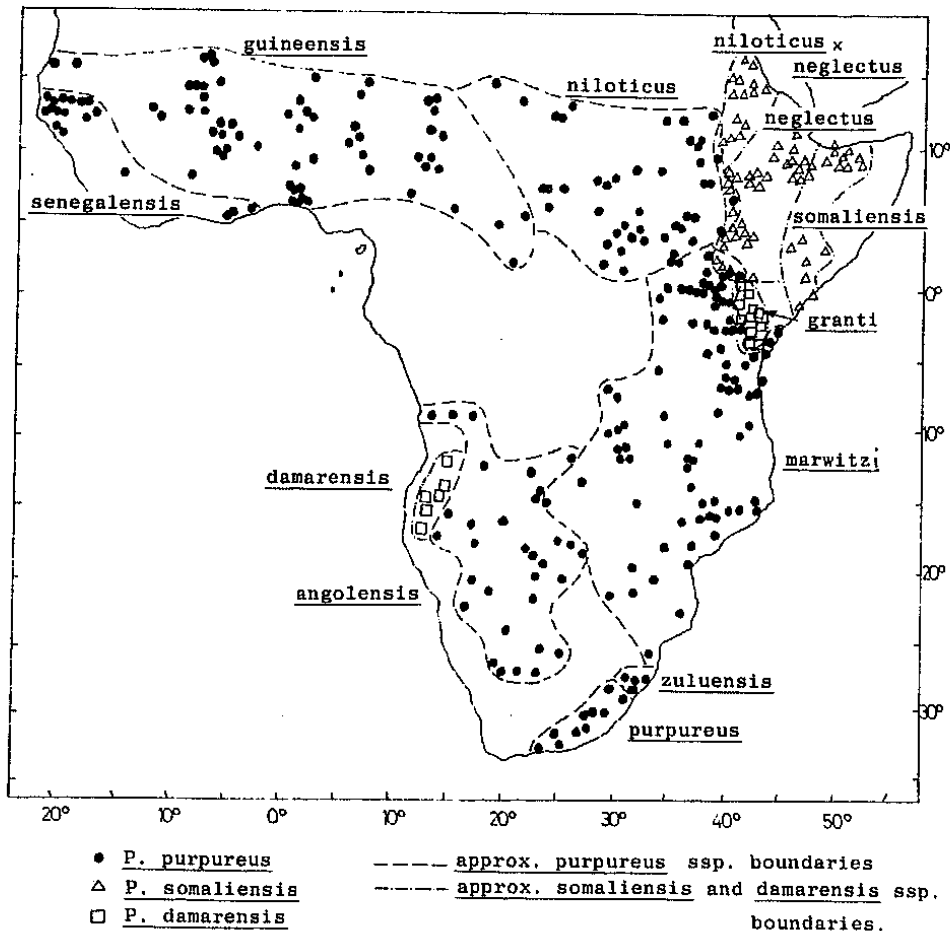
FIGURE 3. Distribution of *P. purpureus*, *P. somaliensis* and *P. damarensis*

Table 1. Classifications of the Phoeniculidae

Peters (1945)		White (1965)		Mackworth-Praed & Grant (1957, 1962, 1970)	
Phoeniculus		Phoeniculus		Phoeniculus	
purpureus (Muller)	erythrorynchus angolensis zuluensis marwitzi senegalensis guineensis niloticus somaliensis neglectus abyssinicus purpureus granti bollei (Hartlaub)	purpureus angolensis marwitzi senegalensis guineensis somaliensis neglectus damarensis granti bollei jacksoni okuensis	purpureus angolensis marwitzi senegalensis guineensis somaliensis neglectus damarensis granti bollei jacksoni okuensis	purpureus angolensis marwitzi senegalensis guineensis niloticus somaliensis neglectus abyssinicus damarensis granti bollei jacksoni okuensis	purpureus angolensis marwitzi senegalensis guineensis niloticus somaliensis neglectus abyssinicus damarensis granti bollei jacksoni okuensis
castaneiceps (Sharpe)		castaneiceps		Scoptelus	
aterrimus (Stephens)		aterrimus		castaneiceps	
Rhynopomastus minor (Ruppell)		minor		brunniiceps	
cyanomelas (Vieillot)		cyanomelas		aterrimus emini notatus anchietae cavei Macdonald Rhynopomastus minor cabanisi	
cyanomelas (Vieillot)		cyanomelas		cyanomelas schallowi	

P. damarensis occurs as two distinct populations: d. granti in north-east Kenya and south-west Ethiopia, and d. damarensis on the Damara-land Plateau of South West Africa. White (1965) lists them as conspecific and adds that they are probably conspecific with P. purpureus. P. damarensis inhabits drier regions than P. purpureus and is restricted to Acacia woodland (Moreau 1966), whilst P. purpureus ranges over more thickly wooded savannas and is especially associated with riparian forest and palms. Moreau suggested that at a period of a little over 10,000 years ago P. damarensis had a nearly continuous range, but with subsequent reduction of Acacia steppe the range fragmented leaving two populations separated by the more habitat-tolerant P. purpureus. P. d. granti is smaller than damarensis and is also more glossy, more blueish purple and has a partly black bill, whilst damarensis is generally dull black with a wholly red bill. In view of the range of variation of P. purpureus, these differences are probably not sufficient for the two populations to be regarded as separate species.

There is some sympatry between d. granti and p. marwitzi in north-east Kenya but no evidence of hybridization; not does d. damarensis interbreed with the parapatric p. angolensis. P. damarensis and P. purpureus must therefore be seen as separate species. Reproductive isolation between d. granti and p. marwitzi will be aided by their different habitats.

P. somaliensis has a black bill in both races somaliensis and neglectus, the bill of the latter being shorter and thicker (Table 2a). Like the other arid forms (P. damarensis), they both have dull plumage. White's (1965) opinion was that a third subspecies abyssinicus consists of hybrids between s. neglectus and p. niloticus, plumage and dimensions being intermediate. P. s. neglectus is sympatric with p. marwitzi and p. niloticus around Lake Turkana (L. Rudolf) and southern Ethiopia. These populations appear sympatric contemporaneously and must be regarded as separate species. P. somaliensis and P. d. granti behave as good species in their zone of contact in central Kenya.

P. bollei. Fig. 5

P. bollei inhabits both lowland and montane forest, and has rather a patchy distribution owing to the fragmentary nature of its habitat. The subspecies vary in the amount of white on the head and in size (Table 2b).

The main differences between bollei and purpureus are the smaller size of bollei, its white head and the lack of white on wings and tail. The voice is similar to that of purpureus - a prolonged chattering - although it is quieter and more resonant in bollei (Chapin 1939).

Whilst parapatric over much of its range due to habitat differences, bollei appears sympatric with purpureus in both West and East Africa.

P. aterrimus AND P. cyanomelas. Fig. 4

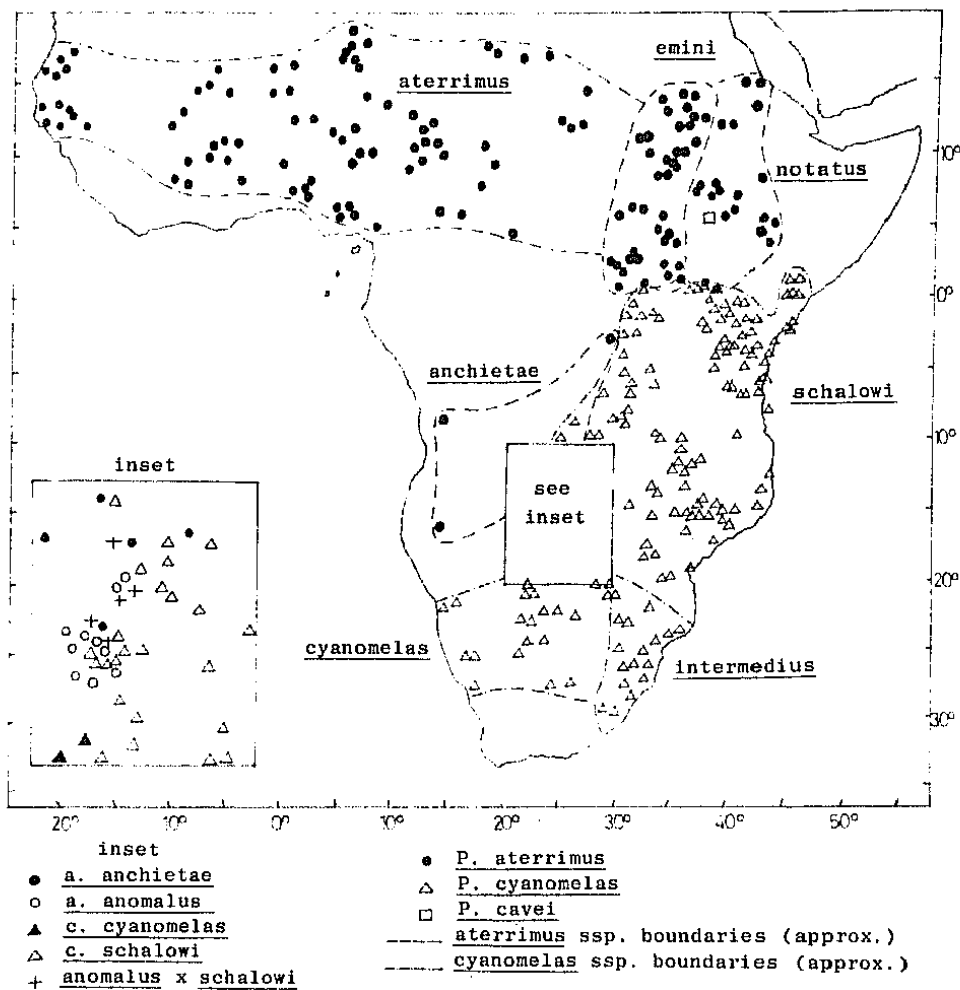
These are small forms, wing mean being c.40 mm less than purpureus (Table 2c). Both aterrimus and cyanomelas inhabit savannas, generally occupying more arid regions than purpureus although there is considerable overlap. Like purpureus, they have dark glossy plumage, iridescence being predominantly violet and steel blue. All forms have a white wing bar, but vary in white subterminal spots on the rectrices. P. aterrimus has a shorter and less graduated tail than cyanomelas (Fig. 2). The bill of cyanomelas is typically long and greatly decurved, whilst aterrimus has a short straight bill (Fig. 1). For this reason they have often been distinguished generically (Mackworth-Praed & Grant 1957, 1962, 1970, Chapin 1939) as Rhinopomastus cyanomelas Vieillot and Scopotelus aterrimus Stephens. There is also a difference in calls (Table 2c). S. cavei (Macdonald 1946) is best included in aterrimus. P. cyanomelas occurs in south and east Africa and aterrimus occupies much of the remaining savanna. Their combined distribution is roughly equivalent to that of the purpureus complex.

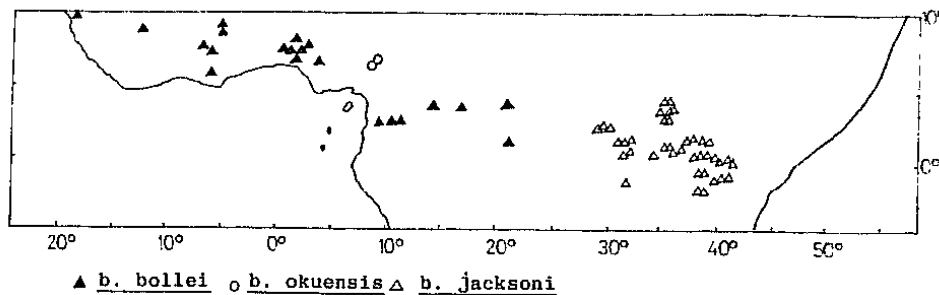
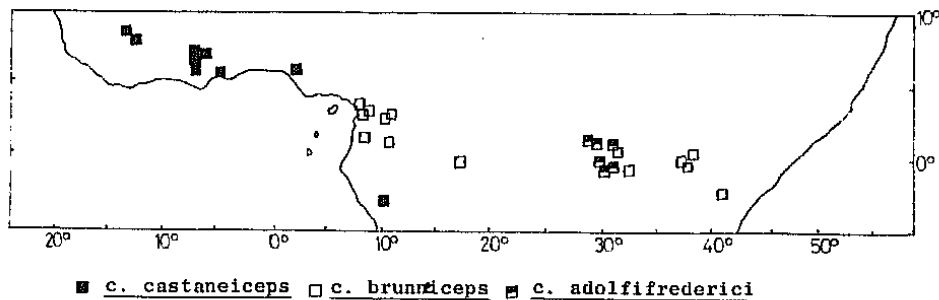
There is some degree of sympatry between aterrimus and cyanomelas, White (1965) noting that they are barely sympatric in Zambia and Angola. Benson & Irwin (1965) have shown a region of hybridisation between a. anomalus and c. schalowi in western Zambia. From this they conclude that aterrimus and cyanomelas are conspecific, and there is almost a continuous range of bill shapes from the typical cyanomelas to the typical aterrimus form (Benson et al. 1971). Any sympatry in northern Kenya is very slight and aterrimus and cyanomelas are probably parapatric there. If there is limited sympatry, differences in voice and feeding ecology (as apparent from the bill morphology) may maintain segregation : schalowi has the most decurved bill of the group.

P. minor. Fig. 5

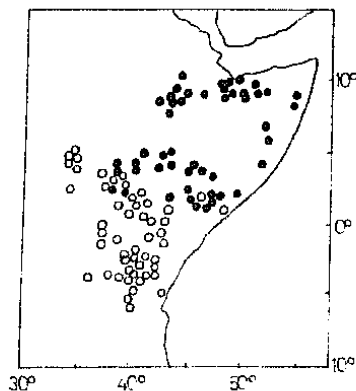
Like P. cyanomelas and P. aterrimus, this is a small species, very like cyanomelas with which it is united in Rhinopomastus by Peters (1945). P. minor occupies the arid bush regions of Ethiopia, Somalia and northern Kenya and is extensively sympatric with both P. aterrimus and P. cyanomelas. P. m. minor and P. m. cabanisi intergrade over much of their range, subspecific differences being in size and white tail spots (Table 2d). P. m. minor resembles P. cyanomelas in the decurved bill, although it is orange in adult minor and black in adult cyanomelas : the bills of juveniles of both species are black.

In the zone of sympatry there appears to be interspecific divergence in plumage pattern : m. cabanisi has neither the white wing bar nor the white tails spots of the sympatric c. schalowi - for these highly mobile species this may be an important means of segregation. The sympatric a. emini and m. minor lack these plumage differences but the bills differ markedly and segregation by feeding ecology probably results.

FIGURE 4. Distribution of *P. aterrimus* and *P. cyanomelas*

a) P. bolleib) P. castaneicepsc) P. minor

- m. minor
○ m. cabanisi

FIGURE 5. Distribution of P. bollei , P. castaneiceps and P. minor

P. castaneiceps. Fig. 5

P. castaneiceps is essentially a bird of secondary growth and forest edge. It is rather secretive, and records are sparse. Smaller than P. bollei (Tables 2b & 2e), it is about the same size as P. aterrimus. Like bollei, the head is paler than the body, the colour varying between the subspecies (Table 2e).

This similarity to bollei seems convergent as they differ importantly in bill shape and colour, leg colour, size, and voice. It appears close to aterrimus with a very similar call (Chapin 1939), the same bill colour and shape and leg colour. It differs from aterrimus in lacking a white wing bar and white tail spots (cf. bollei and purpureus) and in having a longer tail.

P. castaneiceps is mainly allopatric with P. aterrimus, although there appears to be slight sympatry in north-eastern Zaire, and a single record from eastern Kenya suggests sympatry with P. c. schalowi, although there will be habitat segregation.

DISCUSSION AND CONCLUSIONS

In view of the sympatry between P. purpureus and P. somaliensis they must be regarded as separate species; and so likewise must P. purpureus and P. damarensis. The hybridisation between p. niloticus and s. neglectus indicates that the species are very closely allied as do similarities in voice and plumage, and so they are grouped as a superspecies: somaliensis and damarensis can be regarded as arid-zone derivatives of purpureus. All three are highly gregarious although only purpureus has as yet been shown to breed co-operatively (Grimes 1974).

P. bollei has clearest affinities with purpureus and seems to be a forest derivative. It has diverged rather more in habitat, plumage and voice than the members of the purpureus superspecies and is placed in a species-group with this superspecies.

The partial sympatry and hybridisation of aterrimus and cyanomelas similarly indicates a close relationship between separate species, and these two likewise form a superspecies. P. minor, like somaliensis and damarensis, is an arid-zone derivative, but it is not clear whether it is derived from aterrimus or from cyanomelas. It is less closely related than aterrimus is to cyanomelas and in view of the extensive sympatry with these species it is placed in a species-group with the aterrimus superspecies.

Table 2. Characters of wood-hoopoe taxa. (a) P. purpureus,
P. somaliensis and P. damarensis

Subspecies	Wing ♂ (mm)	Tail ♂ (mm)	Bill ♂ (mm)	Plumage	Bill (ad.)
p. purpureus	125-146.5	146-187	41-62	glossy blue, violet, green	red
p. zuluensis	139-147	197-214	55-60	glossy blue, violet, green	red
p. marwitzi	140-161	210-235	54-61	glossy blue, violet, green	red
p. angolensis	141-165	215-265	57-64	glossy blue, violet, green	red
p. niloticus	131-157	201-228	47-54	duller, darker	red
p. guineensis	134-157	200-268	40-57	duller, darker	red
p. senegalensis	143-155	178-253	50-58	duller, greener	black
s. neglectus	139-150	172-216	47-54	dull. Upperside purple and green	except base black
s. somaliensis	148-160	195-232	48-62	dull. Purple	black, slender
d. damarensis	153-164	203-235	44-56	very dull, dark, Purple	red
d. granti	141-149	183-220	42-55	brighter, glossier, bluer	part black

Notes : (1) Females are slightly smaller (2) Legs and feet red in all species (3) White primary bar and white tail spots present in all species - clinal size increase from p. purpureus to p. marwitzi and p. angolensis (4) Voice apparently the same in all species (Benson 1948): prolonged harsh chatter and quiet chuckles

(b) P. bollei

Subspecies	Wing ♂ (mm)	Tail ♂ (mm)	Bill ♂ (mm)	Plumage
b. bollei	130-135	200-222	38-50	Head, throat buffish white; no white on wings and tail
b. okuensis	120-134	165	41	The same but white on forehead and throat only
b. jacksoni	131-142	179-215	35-46	The same but only head white

Notes : (1) Females are slightly smaller (2) Bill, legs and feet red in all subspecies (3) Voice as purpureus but quieter

Table 2 (continued). (c) P. aterrimus and P. cyanomelas

Subspecies	Wing ♂ (mm)	Tail ♂ (mm)	Bill ♂ (mm)	Bill ♀ (mm)	Plumage
a. aterrimus	97-108	110-121	28-35	26-30	glossy violet, steel blue; bill black; white wing bar; no white tail spots
a. emini	95-110	121-132	30-36	26-30	The same but nape and mantle less violet
a. notatus	97-107	118-136	29-39	26-27	as aterrimus but white spots on outer tail feathers only
a. anchietae	108-117	117-125	27-30		as aterrimus but white spots on all except central rectrices
a. anomalus	113-121	145-161	37-39	30-31.5	as aterrimus but bill small
P. cavei					as aterrimus but more blue
c. cyanomelas	108-117	121-140	45-53	36-42	violet, steel blue, green; bill black; white wing bar; no white tail spots
c. intermedius	108-117	155-170			as cyanomelas but some white tail spots
c. schalowi	109-127	154-201	43-49	32-42	as cyanomelas but white tail spots

Notes : (1) *P. cavei* is known only from a juvenile male (Macdonald 1946) (2) *a. anomalus* from Traylor (1964) (3) Legs and feet black in all subspecies (4) Voice : *P. aterrimus* - quiet chattering wha-wha-wha-wha-wha and *P. cyanomelas* - high twittering, chattering and hooi-hooi-hooi.

(d) P. minor

Subspecies	Wing ♂ (mm)	Tail ♂ (mm)	Bill ♂ (mm)	Plumage
m. minor	92-98	95-107	29-35	White wing bar; no white tail spots; bill orange, decurved
m. cabanisi	98-112	108-125	31.5-36	As minor but no white wing bar

Notes : (1) Females are slightly smaller (2) Legs and feet black (3) Voice a low musical trill

(e) P. castaneiceps

Subspecies	Wing ♂ (mm)	Tail ♂ (mm)	Bill ♂ (mm)	Plumage
c. castaneiceps	101-107	165-170	30-32	Head chestnut both sexes
c. brunniceps	94-107	141-165	26-30	Head: ♂ glossy green or pale brown; ♀ brown; juvenile whitish, sexes
c. adolfifrederici	101-110	162-186	27-30	Head pale brown or whitish both /

Notes : (1) Females are slightly smaller (2) Bill, legs and feet black in all subspecies (3) No white in wings or tail (4) Voice very similar to *P. aterrimus*.

P. castaneiceps has characters of both purpureus and aterrimus. However, it does seem closer to aterrimus in respect of leg colour, size and voice and it forms a species-group with aterrimus, cyanomelas and minor. The possession of a dark glossy head by some adults suggests more recent divergence than bollei from purpureus. As castaneiceps occupies forest-edge habitats, limited introgression with aterrimus may have occurred.

Fig. 6 shows the suggested phylogeny of the Phoeniculidae. The ancestral Phoeniculus was probably a savanna form. The division into two groups is that of Phoeniculus, and Scoptelus and Rhinopomastus

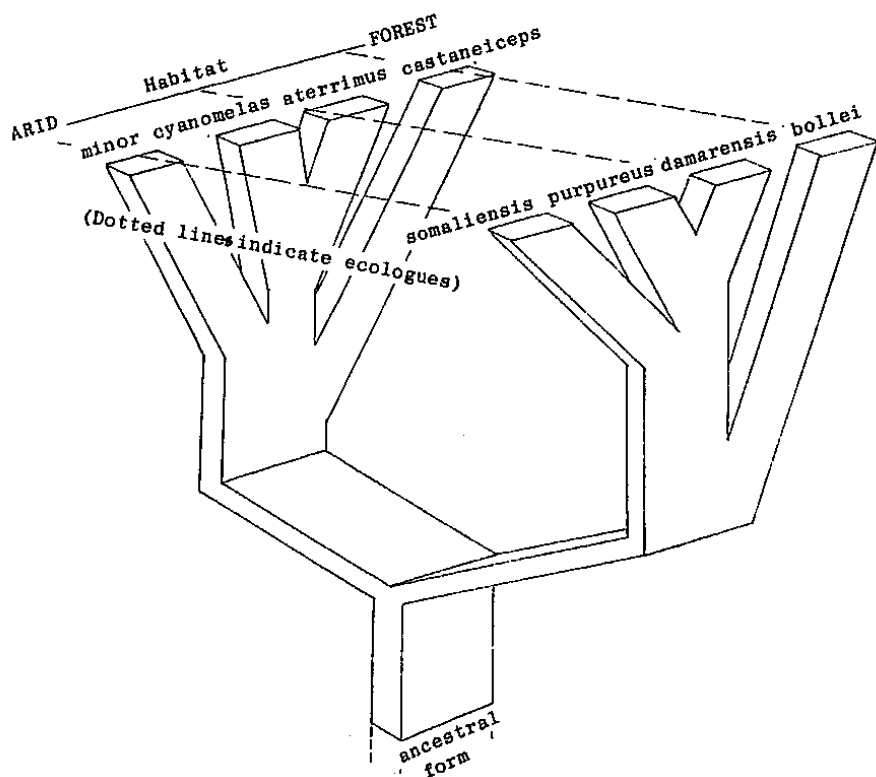


FIGURE 6. Diagrammatic Phylogeny for Phoeniculus

recognised by Chapin (1939) and Mackworth-Præd & Grant (1957, 1962, 1970). As each group now comprises a single species-group, divergence has not been great and it is valid to follow White (1965) in placing all species in Phoeniculus. The size differences may be a result of the ecological necessity for morphological difference between the two related species in the same habitat, as is suggested by Benson et al. (1971) for the differences in bill morphology between purpureus and cyanomelas. This seems valid for size and bill differences in all species of Phoeniculus: the small species feed more on fruit and around flowers than do the larger ones (Moltoni 1940). The sexual dimorphism in the bill shape of P. c. schalowi (Fig. 1b) is a further extension of this phenomenon (Benson et al. 1971).

The white wing bar and white tail spots in gregarious savanna species (purpureus superspecies and minor - Grimes 1974) has probably evolved through the selection pressures of flocking: a flight signal is important for these mobile birds. A reason for the lack of a wing bar in P. m. cabanisi has been suggested earlier. Both P. cyanomelas (Grimes 1974) and P. aterrimus (pers. obs.) join mixed feeding flocks and these generally have a white wing bar also. A continuous contrast signal (the light head) in the less mobile forest species is more important (Davidson 1975): P. bollei is gregarious (Lohrl 1972) and P. castaneiceps joins mixed flocks (pers. obs.). Sociality usually develops from a non-gregarious state (Wynne-Edwards 1962): the ancestral savanna Phoeniculus was probably not gregarious, and contrast plumage developed with increasing sociality. The absence of white on the wings and tail of forest species suggests that they diverged before sociality was well developed.

Subsequent to the divergence of the small and large groups, the radiation has followed essentially the same pattern in both groups, differences in present-day distribution probably resulting from varying divergence times. Relationships will only become clearer when more behavioural and ecological studies have been made. All Phoeniculus species would repay further investigation.

SUMMARY

The evolution and systematics of the Phoeniculidae are reviewed using geographical distribution, morphological, ecological and behavioural characters. Conclusions broadly agree with White (1965) in placing all species in the genus Phoeniculus. Eight species are recognised, having the phylogeny shown in Fig. 6; there are two species-groups of four species, each containing a superspecies, one being purpureus, somaliensis and damarensis and the other aterrimus and cyanomelas.

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