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Morphological Variation in the Sacred Ibis *Threskiornis aethiopicus* Superspecies Complex

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Summary: Skins of ibises attributed to forms within the Sacred Ibis *Threskiornis aethiopicus* complex, *sensu* Holyoak (1970) were examined for variation in 12 morphological characters and measured for four other characters. This investigation revealed significant variation within these characters and that several forms of the ibis showed distinct and diagnostic suites of characters. The study concludes that three species should be recognised *viz. T. aethiopicus, T. melanocephalus* and *T. moluccus* comprising a superspecies complex. It was also concluded that *T. strictipennis* is synonymous with *T. moluccus* and that *T. pygmaeus* is a distinct and dwarfed form of *T. moluccus*. The forms *T. abbotti* and *T. bernieri* are very similar to one another and are most closely related to *T. aethiopicus*. *T. melanocephalus* is distinct from other members of the complex.

Introduction

Various authors have recognised a species complex of the Sacred Ibis *Threskiornis aethiopicus* that includes forms that range from Africa, through southern and eastern Asia and into south-east Asia and Australasia (Steinbacher 1979; Van Tets 1978). This taxon was recommended by Holyoak (1970) who lumped several clearly related forms that had been originally described as *Tantalus aethiopicus* Latham 1790, *Tantalus melanocephalus* Latham 1790, *Ibis moluccus* Cuvier 1829, *I. strictipennis* Gould 1838, *I. bernieri* Bonaparte 1855, *I. abbotti* Ridgeway 1893 and *Threskiornis aethiopicus pygmaeus* Mayr 1931. Other authors (e.g. Roselaar 1977) recognise four distinct species, *Threskiornis aethiopicus, T. bernieri, T. melanocephalus* and *T. moluccus* within the superspecies complex.

In an attempt to resolve the question of the status of these forms this study reviews the morphological variation seen in museum specimens from throughout the ranges of each form. These data are augmented with field studies of birds from South Africa and Australia. Comments on the taxonomy of these forms are given.

Methods

Skins of Sacred Ibis from the following museum collections were examined: Museum of Victoria, Australian National Wildlife Collection, Australian Museum, South Australian Museum, Transvaal Museum, South African Museum, Museum National d'Histoire Naturelle (Paris), American Museum of Natural History, Museum Zoologicum Bogoriense, National Museum and Art Gallery of Papua and New Guinea, Queensland Museum, Institut Royal Des Sciences Naturelles De Belgique, Musee Royal D'Afrique Central, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Cambridge University Museum of Zoology, Forschung Institut Senckenberg Frankfurt, British Museum (Natural History), National Museums and Monuments of Zimbabwe, National Museums of Kenya, Smithsonian Institution, and Rijksmuseum van Naturlijke Historie.

Additional measurements and descriptions of morphological characters were taken from Mayr & Rand (1937), Amadon & Woolfenden (1952), Gyldenstolpe (1955), Benson (1967), Benson & Penny (1971) and Mees (1982).

The following standard measurements were taken from African and Australasian specimens held in museum collections and from birds captured in the field: culmen length (from bill tip to proximal edge of horny bill skin on upper mandible); wing chord; tarsus length; and tail length.

Data were analysed using standard statistical procedures according to Zar (1974) and Siegel (1956) and the BMDP (Dixon 1982) software.

Discussions with many field workers and reference to standard field guides and handbooks were also used

to piece together the distribution of forms within the species complex.

After a preliminary inspection of a range of specimens the following morphological characters (with specified categories), which appeared to allow distinction between forms, were recorded from all specimens: bill silhouette (gracile, intermediate, robust); neck sac (present, absent); straw-like neck feathers (present, absent); nuchal tracts (present, absent); colour of tip of primary wing feather (white, black); colour of tip of secondary wing feather (white, black); extent of lacy tertiary wing feathers (small, large); colour of lacy tertiary wing feathers (white, grey, black); colour of secondary coverts/axillaries (white, yellow); colour of tail feathers (white, yellow); colour of iris (white, blue, brown); and colour of neck feathers of juveniles (white, grey).

Results

The variation in morphological characters and the geographic area of seven forms in the Sacred Ibis species complex are given in Table 1. Within each form there was no variation in any character between all specimens attributed to that form.

Some forms show the same suite of characters. The three Australasian forms *moluccus*, *strictipennis* and *pygmaeus* are virtually identical in the characters that were recorded with the obvious exception that *pygmaeus* is a dwarf form (Table 2). Close examination of all specimens of *moluccus* and *strictipennis* indicates that these forms are identical and that body size varies clinally with latitude.

Similarly *abbotti* and *bernieri* are very similar to each other in the characters that we recorded and are close to, but significantly smaller, than *aethiopicus* (Table 3).

There are also clear differences in the characters exhibited by several forms. For example, *aethiopicus*, *melanocephalus* and *moluccus/strictipennis* are distinctly different from each other and this view is reinforced by observation of birds in the field and in zoo collections. The conspicuous differences are the bill silhouette, neck sac and wing feather colours and patterns. Each suite of these characters allows visual examination to be diagnostic for each of these three forms.

Close examination of specimens from possible contact zones between distinct forms was attempted. There was no intergradation of characters between *moluccus* and *melanocephalus* despite their close contact in the Sulawesi/Moluccan islands area and their distribution is apparently allopatric (White & Bruce 1986). Unfortunately we were unable to locate any specimens from

Table 1 The variation in morphological characters and the geographic area of the seven forms of the Sacred Ibis superspecies complex.

Character	*abbotti*	*bernieri*	*aethiopicus*	*melanocephalus*	*moluccus*	*strictipennis*	*pygmaeus*
Distribution	Aldabra	Madagascar	Africa	Asia	Moluccas	Australia	Rennell Is.
Bill silhouette	gracile	gracile	robust	intermediate	gracile	gracile	gracile
Neck sac	no data	no data	present	absent	absent	absent	absent
Neck straws	absent	absent	absent	present	present	present	present
Nuchal tracts	absent	absent	absent	absent	present	present	present
Tips of 1°	white	white	black	white	black	black	black
Tips of 2°	white	white	black	white	white	white	white
Extent of 3°	large	large	large	large	small	small	small
Colour of 3°	black	black	black	grey	black & white	black & white	black & white
Colour of axillaries	yellow	yellow	yellow	yellow	white	white	white
Colour of tail	white	white	white	yellow	yellow	yellow	yellow
Iris colour	bluish white	white	brown	brown	brown	brown	brown
Juvenile neck colour	white	grey & white	grey & white	grey & white	grey & white	grey & white	grey & white
Sample size	11	23	93	67	36	76	10

Table 2 Body size of Australasian forms of the Sacred Ibis (mean and standard deviation; P = F value from 1-way Analysis of Variance). Note that there were too few female specimens of *pygmaeus* for analysis.

Form	Location	Culmen length (mm)	Wing length (mm)	Tarsus length (mm)	Tail length (mm)	Sample size
Males						
moluccus	Ceram	168 (4)	368 (10)	91 (4)	121 (5)	10
moluccus	PNG	180 (8)	360 (21)	98 (8)	122 (6)	11
strictipennis	Nth Aust	183 (11)	369 (14)	100 (7)	125 (6)	15
strictipennis	Victoria	190 (5)	381 (13)	99 (6)	—	18
F value		$P < 0.001$	$P < 0.01$	$P < 0.05$	$P > 0.05$	
pygmaeus	Rennell	123 (9)	304 (23)	74 (8)	110 (12)	6
F value		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	
Females						
moluccus	Ceram	139 (10)	348 (7)	83 (6)	115 (6)	8
moluccus	PNG	141 (14)	333 (5)	86 (7)	116 (3)	4
strictipennis	Nth Aust	148 (9)	349 (10)	83 (5)	118 (5)	9
strictipennis	Victoria	151 (8)	355 (10)	85 (4)	—	35
F value		$P < 0.01$	$P < 0.001$	$P > 0.5$	$P > 0.1$	

Table 3 Body size of African forms of the Sacred Ibis (mean and standard deviation; P = F value from 1-way Analysis of Variance). Note that there were too few male specimens of *abbotti/bernieri* for analysis.

Form	Location	Culmen length (mm)	Wing length (mm)	Tarsus length (mm)	Tail length (mm)	Sample size
Males						
aethiopicus	Sudan	169 (7)	375 (14)	99 (4)	138 (19)	12
aethiopicus	Zaire	169 (8)	377 (13)	99 (6)	133 (6)	29
aethiopicus	Zambia	178 (4)	377 (4)	101 (4)	127 (12)	7
aethiopicus	S Africa	180 (8)	378 (18)	102 (6)	149 (6)	40
F value		$P < 0.05$	$P > 0.5$	$P = 0.5$	$P > 0.1$	
Females						
aethiopicus	Sudan	139 (8)	357 (11)	89 (6)	131 (10)	19
aethiopicus	Zaire	142 (6)	358 (13)	88 (4)	129 (8)	23
aethiopicus	Zambia	141 (5)	362 (10)	94 (6)	142 (6)	8
aethiopicus	S Africa	152 (6)	363 (9)	91 (5)	146 (4)	53
F value		$P > 0.5$	$P > 0.5$	$P < 0.05$	$P < 0.001$	
abbotti	Aldabra	124 (5)	337 (10)	71 (3)	136 (5)	8
bernieri	Madagascar	135 (5)	337 (6)	75 (3)	131 (5)	7
F value		$P = 0.001$	$P > 0.5$	$P < 0.01$	$P > 0.1$	

areas where *aethiopicus* and *melanocephalus* might make contact in the Middle East. However, there was no evidence of any merging of characters in specimens from near the possible contact zones. We also failed to find any evidence that the forms overlap in their breeding ranges.

Discussion

This study has revealed through simple methods that there is considerable variation in morphological characters within the *Threskiornis aethiopicus* superspecies complex and that several forms show distinct suites of characters which are diagnostic.

The study supports Mees' (1982) conclusions that *T. moluccus* and *T. strictipennis* are identical forms and should be synonymised. The name *moluccus* has priority. Holyoak's (1970) study is marred because of the limited material available to him. He distinguished between *moluccus* and *strictipennis* on the basis of the colour of the shafts of the secondary wing feathers. Our field studies of a population of *strictipennis* have shown this character to be variable between birds and probably with the age of the bird. Museum specimens of *moluccus* show similar variation between birds.

Threskiornis pygmaeus is identical to *T. moluccus* except that *pygmaeus* is a dwarf form significantly smaller than expected from the clinal variation in body size that is shown by *moluccus*. We would recommend taxonomic distinction between these two forms but have no data to determine the level of the forms. They could be treated as subspecies of the same species.

Threskiornis abbotti and *T. bernieri* are very similar and could be considered as one form (*bernieri* has priority over *abbotti*). Their relationship to the other forms is unclear but they could be seen as an isolated subspecies of the African form. Further work is needed to determine their taxonomic status.

Holyoak (1970) merged the forms *aethiopicus*, *melanocephalus* and *moluccus* because he regarded their similarities as 'almost certainly too great for them to act as separate species if their ranges were to meet...'. We found these forms to be distinct despite examining many more specimens from a wider geographic area than were available to Holyoak (1970) and there appears to be no intergradation in characters between them. We conclude that these forms are separate species and we recommend that they be recognised as three closely related but distinct species.

The potential for inter-breeding between the forms may be assessed by studies of courtship displays (Lorenz 1941; Tinbergen 1959; Kahl 1971) where the courtship displays suggest that pre-mating isolation (*sensu* Littlejohn 1969) may be occurring between forms. We attempted to document the courtship displays in populations of *aethiopicus* and *strictipennis* but were not successful. Although the behaviour of the forms is strikingly different we were not able to confirm the homology between the displays shown by each form. We would encourage further work in this area of interest.

The morphological distinctiveness of *aethiopicus*, *melanocephalus* and *moluccus* recorded here seems to also be reflected in differences in the cytogenetics of these forms. De Boer & Van Brink (1982) investigated the somatic karyotypes of these forms and found that each karyotype was distinctive. These authors concluded that *moluccus* may have been the ancestral form from which *aethiopicus* and *melanocephalus* were derived independently.

Based on morphological and cytological evidence we conclude that there is good reason for recognising three species within the *Threskiornis aethiopicus* complex. The taxonomic status of the forms *bernieri* and *abbotti* is less clear to us and warrants further work. We would recommend the following taxonomy:

Threskiornis aethiopicus aethiopicus
Threskiornis aethiopicus bernieri
Threskiornis melanocephalus
Threskiornis moluccus moluccus
Threskiornis moluccus pygmaeus.

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