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VARIATION IN THE AUSTRALIAN KINGFISHERS (AVES: ALCEDINIDAE)

BY ALLEN KEAST

(Figure 1)

(Manuscript received 17.12.56)

The present work has as its objective a study of infraspecific variation and speciation in the Australian Alcedinidae.

Species and Range: There are ten species of kingfishers in Australia, and they fall into five genera. Dominant, and the most widespread, are the forest kingfishers (*Haleyon*), of which there are four species. Two "giant" kingfishers (*Dacelo*) do much of their feeding on the ground. Two small, long-billed, short-tailed river kingfishers (*Aleyone*), single members of the New Guinea genera *Tanysiptera* (long-tailed kingfishers) and *Syma*, make up the rest of the fauna.

In terms of distribution and habitat the kingfishers separate out as follows: Syma torotoro and Tanysiptera sylvia, confined to rain-forests and scrubs of the north-eastern corner of the continent; Alcyone pusilla and Halcyon chloris, mangroves and inlets of the north; Halcyon macleayi, rain-forests and sclerophylls of the east; Alcyone azurea, rivers of the east and north; Halcyon sancta, migratory species (in the south) with a wide range, but concentrating for breeding in the better sclerophylls and savannahs; Dacelo novaeguineae and Dacelo leachii, southern and eastern sclerophylls and savannahs in the case of the former and northern savannahs in the latter; Halcyon pyrrhopygia, an inhabitant of the dry interior of the continent. Where more than one kingfisher occurs over a section of the continent different vegetation associations are occupied or food requirements are distinct. In the south-eastern sclerophyll forests, for example, the forest Halcyon sancta and Dacelo novaeguineae obviously have different ecological requirements (the former is much smaller, having a wing-length of 90-100 mm, the latter being 215-230 mm). The water kingfisher, Alcyone azurea, obtains its food exclusively by diving.

The bulk of Australian species has obviously had a northern origin, in several instances in the not too distant past. Tanysiptera sylvia and Syma torotoro are New, Guinea species with a mere toehold in the tropical north-eastern corner. Alcyone pusilla, another northern species, is restricted to the mangrove-fringed shoreline of the Australian north coast. Halcyon sancta, extending widely over Australia, and H. chloris of the northern mangroves, are members of superspecies extending from Asia to the south-west Pacific. Both are migrants in Australia, suggesting that their occupation of the continent is too brief for them to have become adapted to the temperature and food conditions of winter in the south. Halcyon maeleayi, an eastern and northern forest species in Australia, is also a migrant in the south of its range.

Species endemic to Australia and that obviously originated here are *Halcyon pyrhopygia* and the two members of the genus *Dacelo*. *H. pyrhopygia* is perfectly adapted to life in arid places, whilst both kookaburras (*Dacelo spp.*) extend well inland. *Alcyone azurea* has presumably had a long occupation of the continent for, despite its belonging to a tropical group, there is no migration even in cold areas.

Material and Methods: Specimens in the following museums were used in the work: American Museum of Natural History, New York (which houses the Mathews "types"); Australian Museum, Sydney; National Museum of Victoria, Melbourne; South Australian Museum, Adelaide.

Localities from which specimens of the various species have been seen are listed in the taxonomic section. Measurements of specimens were made as follows: *Wing-length*—from angle of wing to tip, straightened along the rule; *Bill-length*—from tip to the base of the first feathers; *Tail-length*—from base of centralmost two feathers to the tip.

The approach in the present work has been to study geographic variation in series of adult male specimens and to confirm any trends with the adult females. Detailed measurements of the former are set out in the body of the text. In the case of migratory and nomadic species only specimens collected during the breeding season have been used. Specific descriptions, plus those of sex and immature forms, are not given as they have been amply covered in the various standard works on Australian ornithology. It may be mentioned,

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however, that with the exception of Dacelo leachii and Syma torotoro, sexual dichromatism is negligible in Australian kingfishers. The sexes, moreover, tend to be of the same general size (judging from wing lengths) as will be seen from the following:-

	Males			Fem	ales
Halcyon sancta (Sydney area) (15 males,	00-08	(94)	mm	88-96	(94) mm
H. macleayi (N.S.W.) (10 and 6) \ldots	88-96	(93)	mm	92-95	(94) mm
Dacelo novaeguineae (N.S.W.) (10 and 5) 2	15-230	(222)	mm	218-227 195-205	(223) mm (100) mm

Immature kingfishers are, as a rule, readily recognisable on plumage characters. Buff edging to the wing coverts and feathers of the forehead occurs in the young of Haleyon, and a general drabness is typical of most species at this time. However, the significance of the breast colouring and ventral barring in the individually variable Dacelo leachii requires proper study from the age viewpoint.

When geographic variation in a species has been detected special attention has been given to ascertaining whether it was merely clinal variation (gradual change of character from one end of a range to another) or whether isolation had been involved in its development. Isolation is, of course, the first step in the process of speciation. Attention has also been given to factors governing distribution and to the nature of distributional barriers, present and past. Forms with the potential of developing into species in the future are discussed. Finally, recommendations are made as to how infraspecific variation may best be treated nomenclatorially.

Alcyone azurea (Latham) 1801. (Azure Kingfisher).

This little river kingfisher ranges along the north coast from Derby in the north-west to Cape York, and thence south to Tasmania and the Mount Lofty region of South Australia. In the south-east it extends inland along the rivers. Beyond Australia the species has an extensive distribution in New Guinea and the contiguous islands.

A. azurea is a true water kingfisher, living along rivers and small creeks and obtaining its food by diving. Minor range gaps are to be expected where waterways are absent, although over much of the north of the continent it inhabits mangroves, a reasonably continuous habitat.

Geographic variation: Two basic types occur: south-eastern Australia (azurea) and north Australia (Cairns-Kimberleys) (pulchra). The latter is distinguished by being a deeper (royal) blue dorsally and having the breast more richly coloured (deep chestnut in northwestern birds), and with purplish-blue extending down the flanks, as has been noted by Sharpe, Hartert, Mathews (1918) and North (1909).

Birds from Tasmania, Victoria, and the Mount Lofty Ranges, fit into the Sydney series. The deeper blue dorsal colouring of the northern birds is first suggested in odd individuals from northern New South Wales (specimens in American Museum of Natural History), suggesting that, so far as dorsal colouring is concerned, the change from southern to northern type is clinal. All Cairns birds have the richly coloured back, as do those from Cape York. Three McArthur River birds and one from Groote Eylandt (Gulf of Carpentaria), have drabber (blackish) back and the rump a paler blue than typical northern birds and they approach the southern birds in these characters. Again, birds from southern New Guinea are a shade deeper blue on the back than those from northern Australia.

In contrast to the colouring of the dorsal surface that of the ventral surface only becomes really richly coloured (deep chestnut) in birds from the Northern Territory and Kimberleys.

A. azurea has a south-north cline of decreasing size, as will be seen from the following wing-length measurements for adult males: Mount Compass, South Australia (1), 75 mm; Wing-length measurements for adult males: Mount Compass, South Australia (1), 75 mm; Glenelg River (1), 75 mm; Tasmania (4), 79-82 mm (mean 81); Melbourne area (6), 74-80 mm (76); Sydney area (16), 75-80 mm (77); Richmond River—Brisbane (6), 76-79 mm (73); Cairns (8), 76-79 mm (73); Cooktown (the "type"), 75 mm; Cape York (5), 73-75 mm (73); McArthur River (3), 71-74 mm (73): Groote Eylandt (1), 72 mm; Melville Island (1), 74 mm; coastal Northern Territory (5—two from King River, one each from Port Essington, Alligator River, Victoria River), 72-74 mm (73); Parry's Creek (3—including "type"), 71-73 mm (72); Napier Broome Bay (2), 72 and 75 mm; Derby (4), 72-75 mm (74). Five males from southern New Guinea (Fly River and Milne Bay) have wings ranging from 73-75 mm (74). 73-75 mm (74).

Northern birds also have shorter tails, viz.: Tasmania, 32-37 mm (35); Melbourne, 32-37 mm (34); Sydney, 32-36 mm (34); north-eastern New South Wales, 33-36 mm (34); Cairns, 31-34 mm (33); Cape York, 26-30 mm (28); coastal Northern Territory, 28-31 mm (30); Parry's Creek and Napier Broome Bay, 30-32 mm (31); Derby, 28 and 29 mm.

North-western birds have shorter bills than the eastern stock, as pointed out by Hartert (see Mathews). There is a great deal of individual variability in the bill of kingfishers, hence large series would be necessary to demonstrate accurately the extent of this difference.

At one time or another the following races have been proposed in Australia: diemenensis Gould 1846 (Tasmania); victoria Mathews 1912 (Frankston, Victoria); azurea (Latham) 1801 (Sydney); mixta Mathews 1912 (Cooktown, Queensland); pulchra Gould 1846 (Port Essington); alisteri Mathews 1912 (Parry's Creek). The names victoria, mixta, and alisteri, were subsequently placed in synonymy by their author. Tasmanian birds do not differ in colour from those of the mainland, as Gould originally supposed, but they are, in fact, slightly larger, representing the endpoint of a size cline. They should not bear a subspecific name.

The form *pulchra* is a distinctive one. The question arises as to whether the name should be restricted to north-western birds (chestnut breasts), or apply to northern birds as a whole (backs a deep blue, small size), as Mack (1953) has done. The writer feels, however, that the proper course is to recognise three races, an eastern and southern one (*azurea*), a north-eastern one (which will take the name *mixta* Mathews 1912), and a north-western one (*pulchra*).

The north-western and eastern populations of *A. azurea* are apparently isolated. Despite absence of differentiation the Tasmanian and Mount Lofty (South Australia) populations are probably isolated from the main eastern stock. Likewise the New Guinea-Aru populations (three New Guinea races are listed by Mayr, 1941), are presumably isolated from those of Australia.

Alcyone pusilla (Temminck et Laugier) 1836. (Little Kingfisher).

This small mangrove inhabitant extends along the north coast from about Hinchinbrook Island to Port Keats. It is a sedentary species.

Geographic variation: There are two colour-forms. Hinchinbrook-Cairns birds (halli Mathews 1912) are a deep royal blue above, with a greenish-blue developed to a variable extent on the forehead. North-western birds (Melville Island, Anson Bay, King River) are distinctly paler blue above (ramsayi North 1912). Cape York birds (given the name yorki by Mathews 1918), and those from Groote Eylandt, have hybrid characteristics, with individuals matching each colour form and others being intermediate. Thus two Cape York birds resemble those from Melville Island, four are intermediate, and one is purplish-blue above (specimen from Somerset in the far north). The two Groote Eylandt birds are intermediate.

Birds from southern New Guinea are an even deeper purplish-blue above than Cairns birds. It would seem likely that the richly-coloured Somerset bird derives its characteristics from the New Guinea race (*i.e.*, there is gene flow across Torres Strait) rather than from the Cairns one well to the south.

Wing-length measurements for adult males are: Hinchinbrook (1), 58 mm; Cairns (9), 53-56 mm (54); Cape York (4), 51-53 mm (52); Daru and Wassi Kussa River, New Guinea (5), 50-53 mm (51); Melville Island (5), 51-53 mm (52); King River (3), 51-53 mm (52). Tail-lengths reflect the wing-length changes, the Hinchinbrook male measuring 22 mm; Cairns birds 20-21 mm (21); Cape York, all 20 mm; southern New Guinea, 18-20 mm (19). Thus a south-north cline of decreasing size is indicated.

Syma torotoro flavirostris Gould 1850. (Yellow-billed Kingfisher).

In Australia Syma torotoro is restricted to the northern tip of Cape York. It is described as an inhabitant of the tropical brushes by MacGillivray (1918). However, Thorpe (1909) says that it frequents the dry, open belts of timber inland and is seldom met with in the dense coastal scrubs.

Geographic variation: The Australian race constitutes a distinctive isolate (on colour grounds). Wing-length measurements of adult males (5) are: 75-78 mm (76), and females (4): 74-76 mm (75).

S. torotoro has apparently been some time in Australia for it is difficult to say from which of the races inhabiting southern New Guinea the Australian form *flavirostris* is derived. The race *pseutes* from the Oriomo is much more rufous ventrally, this colour extending up towards the chin and right down over the abdomen, whereas in *flavirostris* the rufous is only strongly developed on the breast and upper abdomen. The Oriomo birds are dark green above, much brighter than the drab colouring of *flavirostris*. Specimens of the form *brevirostris* from the Wassi Kussa River have the ventral red as extensive as in *pseutes* but it is paler; the back is drab like *flavirostris*. A pair of birds from the Aru Islands have the ventral colouring of the Oriomo *pseutes* (*i.e.*, rich and extensive) with the back somewhat drab (but not as much so as in the Wassi Kussa birds).

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Dacelo novaeguineae¹ (Hermann) 1783. (Kookaburra).

The Kookaburra is an inhabitant of the sclerophyll and savannah woodlands of the eastern section of the continent from west of Adelaide to Cape York. Whilst it extends through the drier country in the south where the range overlaps that of *D. leachii* it is essentially an inhabitant of the coastal mountains. For example, Thomson (1935) states that in Cape York *D. novaeguineae* is dominant in the hilly country of the central range of the Peninsula (the only place where the southern *Gymnorhina tibicen* and *Strepera graculina* also occur), whilst *D. leachii* is the common species elsewhere (drier areas). The susceptibility of *D. novaeguineae* to heat and drought (Austin 1909, and others) might be noted: possibly this places it at a competitive disadvantage with *D. leachii* in the north of the continent.

The Kookaburra has been introduced to both the south-west of the continent (Serventy and Whittell 1951) and Tasmania (Sharland 1945), in both of which the species is now wellestablished.

Geographic variation: This is individually a variable species, though the sexes are alike in colouring. Adults have been seen from Adelaide (few), Melbourne and Sydney (each good series), Clarence and Richmond Rivers, Leeton and Mossgiel (single birds), Cairns (series), Cooktown, Cape York (series). The species does not appear to vary geographically in colour.

Measurements	for	adult	males	from	various	parts	\mathbf{of}	the	range	are:
				Wing	Length	(mm)	T	ail L	enoth ((mm)

Tan Long m (mm			
))			
£)			
1)			
<i>)</i>)			

It will be seen that whilst there is minor size variation (as judged by wing-length) from Melbourne to Cairns, there is a sharp drop as between the Cairns and Cape York populations at the northern extremity of range. The bill of Cape York birds is also shorter than in birds from the south. The difference between Cairns and Cape York birds is such as to be strongly suggestive of isolation (former or continuing) between them.

The small northern form of *Dacelo novaeguineae* must be recognised nomenclatorially. As, however, only one bird from Cooktown has been available to me I am unable to say what the southern limits of the form are. This is important as the name *minor* Robinson 1900 was given to Cooktown birds and *mclennani* North 1911 to those from Cape York. The name *minor* is the older and, since the single Cooktown bird is quite small, I recommend its usage pending further investigation. Mathews' "*tregellasi*", given to the Victorian birds, must be reduced to synonymy.

Dacelo leachii Vigors and Horsfield 1827. (Blue-winged Kookaburra).

This species ranges across the north of the continent (where there is savannah woodland) from about Toowoomba, south Queensland, to south of Carnarvon in the mid-west (see Fig. 1). Ninety-Mile Beach, to the south of the Kimberleys, apparently forms a distributional barrier in the west. Beyond Australia *D. leachii* ranges along the south coast of New Guinea from the Mimika to Port Moresby, the island stock being divisible into two races (Mayr 1941).

Dacelo leachii is a sedentary species.

Geographic variation: D. leachii is most variable, both individually and geographically. Much of the individual variation is apparently associated with age. Sexual dimorphism in colour is pronounced in D. leachii, the tail of males being blue (above) and those of females cinnamon with blue barring.

At the geographic level *D. leachii* is divisible into many races. The coloration of the different parts of the body varies independently as follows:—

(a) Back: This is dark chocolate brown in birds from Melville Island and adjacent parts of the Northern Territory, slightly paler in Cape York birds, and fairly dark in birds from Cairns and Groote Eylandt. Populations elsewhere are distinctly paler and could be described as mid-brown, though there is individual variability. New Guinea birds (Hall Sound, Port Moresby) are much darker dorsally than any in Australia and sometimes have a "bluish" tint through the mid-back.

¹ Several authors (recently Condon, Mack) have stressed the inaptness of *novaeguineae* (see Streseman) as the specific name for the Kookaburra, since it does not occur in New Guinea. It is a pity, after such long usage, to drop *gigas* in favour of *novaeguineae*. A recent paper (Lysaght 1956) has shown that the type specimen of Sonnerat did, in fact, come from eastern Australia.

(b) Breast: This is more reddish in Melville birds than those from elsewhere. Specimens from Port Essington and Port Charles are also richly coloured. The breasts are paler ("ochraceous") in birds from the southern extremity of range in the west (Carnarvon, Roeburn, Yalbalgo, Boolathanna). Kimberley birds, and those from the drier areas of the Northern Territory are most variable, and in a sense intermediate since about two-thirds of those examined had breasts of intermediate tones, a third had ochraceous ones. Some, especially the few from Parry's Creek, were quite pale.



Fig. 1.—Races of the Blue-winged Kookaburra (Dacelo leachii): (1) clijtoni, (2) leachii leachii, (3) cervina, (4) kempi, (5) intermedia and superflua. The heavy black lines indicate distributional barriers.

Eastern birds are pale ventrally, the colouring in birds from Cairns and further south being best described as pale buff. Normanton and McArthur River individuals are almost as pale. The Cape York series is, however, variable. Two out of nine birds have "ochraceous" breasts and the others are pale. New Guinea birds from Hall Sound and Port Moresby are very pale ventrally.

Whilst the individual variation in breast colouring would suggest that it has an age basis there is some sorting out geographically.

(c) Barring on ventral surface: This is strongly developed in eastern and northern birds, faint or absent in birds from the Kimberleys and Hamersley regions. To some extent it seems to be associated with age.

(d) Blue on wing: The intensity of the coloured area varies somewhat, being brightest in the north (Melville Island, Northern Territory coastal, and Cape York).

In New Guinea birds (Hall Sound and Port Moresby) it is of a slightly richer and deeper shade.

(e) Colouring of top of head: This, in the main, reflects the width of the brown stripe down the centre of the individual feathers. Where it is broad the birds are brownheaded and where narrow, white. Tone of the brown varies, in addition, with the colouring of the back. Over the greater part of the range the top of the head could be said to be "mid-brown" in colour and decidedly streaked. In the far north (Cape York, coastal Northern Territory and especially Melville Island) the colouring is a uniform dark chocolate brown. In the Hamersley populations (south of Ninety-Mile Beach) in western Australia the top of the head approaches white in colour.

Wing-length measurements of adult males from various parts of the range are: South and central Queensland (Brisbane River, Fitzroy River, Duaringa, Double Island)—6 birds, 204-216 mm (208); Cairns (4), 197-206 mm (203); Cooktown (1), 190 mm; Cape York (5), 195-203 mm (198); Normanton (5), 192-200 mm (199); Groote Eylandt (1), 187 mm; Melville Island (4), 178-184 mm (182); Port Essington (3), 180-185 mm (183); other localities in Northern Territory (Port Keats, Katherine River, Daly River, King River—8), 188-196 mm (191); Kimberleys (Parry's Creek, Wyndham, Ord River, Derby—10), 190-196 mm (193); Hamersley area (6), 192-203 mm (197); New Guinea (Goldie River, Hall Sound—5); 202-211 mm (208).

Tail-length measurements reflect those of the wings, being greatest in birds from south-central Queensland (mean 129 mm), with a cline northwards to Cape York (mean 125 mm), and smallest in the Melville Island stock (mean 108 mm), with a cline of increasing size southwards to the Hamersley region (mean 128 mm). The largest bills occur in southcentral Queensland birds (mean 72 mm), with the mean of the Cape York stock 64 mm, and the smallest on Melville Island and adjacent coast (57 mm). Mean bill length of the Hamersley stock is 66 mm.

Summary of geographic variation in D. leachii: It is obvious that there are quite a number of characters varying independently in this species and that, since the species extends through the drier country, most variation must be clinal.

The following geographic forms can be recognised, and their range is plotted on the text figure:

(1) Hamersley region, mid-western Australia (*cliftoni*).—This is a distinctive isolate, readily recognisable by its white head. The presence of one or two "pale-headed" birds in the Derby series indicates that there is slight intrusion of Hamersley genes to the north.

(2) South Queensland to the Gulf of Carpentaria, Northern Territory and Kimberleys (*leachii leachii*).—This is the generalized form of the drier parts of the species range. There is clinal variation, including a south-north cline of decreasing size and darkening of the upper parts in areas of high rainfall (Cairns).

(3) Melville Island and narrow coastal strip on adjacent mainlaind (*cervina*).—This is characterized by the very dark brown upper parts and dark head, also by very small over all size and bill. It is undoubtedly connected with *leachii* by a cline but it must be a steep one. The question arises as to whether to include the Port Essington-Port Keats birds with those from Melville Island (which seems the better course) or stress the differences of the former (smallness, darkness, reddish breast) by keeping it apart from mainland stock. The impression gained from studying the material is that the Melville stock is partly isolated but with gene flow outwards on to the adjacent coast. The "steep" colour changes presumably reflect the precipitous reduction in rainfall from the coast inland in this area of the Northern Territory. The darker mainland birds, *e.g.*, Port Keats, would then be no more than local colour forms.

(4) Cape York (*kempi*).—This bird is fairly small, is dark above but tends to be pale ventrally. Presumably its similarity to *cervina* dorsally reflects like environments in Cape York and Melville Island.

(5) Southern New Guinea (*intermedia* and *superflua*).—The former is much darker dorsally than *cervina* or *kempi* and the blue of the wing is brilliant. It is a large form (wings of male, 202-212 mm, as against 197-203 mm for Cape York; tails 129-132 mm compared to 121-128 mm). New Guinea birds are isolated from those of Australia.

Variation in *D. leachii* may be summed up by saying there are two good isolates (*cliftoni* and the New Guinea *intermedia-superflua*) a partial isolate on Melville Island, and marked clinal variation over the rest of the range.

The number of "races" described in *Dacelo leachii* stems from its marked variability and the fact that its colour is, apparently, readily influenced by physical environment. The following may now be placed in synonymy: *occidentalis* Gould 1870 (Derby); *mungi* Mathews 1912 (Mungi); *nana* Mathews 1912 (Melville Island); *macarthuri* Mathews 1918 (McArthur River).

Halcyon pyrrhopygia Gould 1840. (Red-backed Kingfisher.)

This species is distributed through the inland areas of the continent, extending to the sea in the west, north, and north-east, where the dry country reaches the coast. It does not occur in Tasmania. The habitat could be described as savannah, mallee, and mulga. The range is continuous.

H. pyrrhopygia is a migrant in the south, returning in September to Mudgee, Cobborah, Mossgiel and Broken Hill in western New South Wales, and not being seen after February (Mossgiel, N.S.W., and Laura, S.A.)—see North (1909). Like many other inhabitants of the arid interior the number of birds breeding in an area varies with the season and nomadism is well developed at other times of the year.

Geographic variation: Specimens have been seen from the following localities: Victorian mallee; western New South Wales (Narrabri, Moree, Byrock, Cobborah); Queensland (Charleville, Nogoa River, Coopers Creek, Normanton, Cape York); Northern Territory (Hamilton Bore, Love's Creek, Wantapilla Swamp, Finke River, in the central areas and Brocks Creek, Patrick River, Daly River, McArthur River, in the north); Western Australia (Parry's Creek, Forrest River, Napier Broome Bay, Derby, Marngle Creek, Point Cloates, Geraldton, Marble Bay, Carnarvon, Kalgoorlie).

Geographic variation is negligible. Birds from Parry's Creek (Mathews' "obscurus") are not duller above than those from the south-eastern extremity of range, as stated by Mathews. The chestnut of the rump is actually slightly deeper (freshly moulted birds) in some five specimens of the former. In immature birds from Parry's Creek the characteristic pale tips to the wing feathers are chestnut, compared to buff in Normanton birds of similar age (the only area from which comparable material has been seen). Mathews named the birds from Cape York as a race and subsequently reduced them to synonymy. This was the correct course as other series share the characters attributed to them.

Wing-lengths for series of adult males from various parts of the range are: Port Angusta (4), 102-107 mm (105); Victorian mallee (6), 102-106 mm (103); western New South Wales (9), 100-108 mm (103); Dawson River (1), 103 mm; Port Denison (2), 106 and 107 mm; Normanton (3), 98-102 mm (100); McArthur River (1), 101 mm; Cape York (2), 98 and 99 mm; central Australia (4), 101-104 mm (102). Material from the western section of the continent is poor: Kellerberin (1), 101 mm; Geraldton (1), 99 mm; Point Cloates (1); 103 mm; Carnarvon (4), 98-106 mm (101); Derby (1), 102 mm; Parry's Creek (4), 97-102 mm (100). It will be noted that there is a suggestion of a minor south-north cline of decreasing size in the east.

No races can be recognised in Halcyon pyrrhopygia.

Halcyon macleavi Jardine and Selby 1830. (Macleav Kingfisher.)

This is a species of the coastal and near-coastal sclerophyll and rain-forest in the east and of savannah woodland in the north. The range extends from about the Macleay River (one record for Sydney) to Cape York and thence westwards along the north coast to about Derby. Presumably distinctive eastern and north-western forms are isolated. However, MacGillivray (1914) states that he noted the species all the way down the Cloncurry River, at the head of the Gulf of Carpentaria.

The species is generally considered to be migratory in the south-east, rarely being noted in the southern parts of its range during the winter. There are, however, several birds from New South Wales in the American Museum Collection collected between May and August (Mayr 1937). North (1909) states with respect to New South Wales: "The birds are chiefly migratory, arriving very early in September, a few remaining during the winter." Mayr gives the extra-Australian winter range as Kei Islands, eastern New Guinea (east of Mimika River and Astralobe, Bay), Fergusson Island, the Trobriands, Woodlark, Misima and Tagula, and New Britain. It is apparently a rare bird on the east coast of New Britain for during nearly a year's stay in the Jacquinot Bay area during the war the writer saw only odd birds on perhaps a dozen occasions. The first record was 15 April and the last 1 August.

Geographic variation: Australian birds, collected during the spring and summer, fall into[#] two colour series—those from the north-west and east of the continent respectively. Variation in *H. macleayi* is in two main characters, size of the "white panel" on the wing and tone of blue of the dorsal surface, as has been shown by Mayr (1937).

The white area on the wing is much more extensive in north-western birds than in eastern, e.g., out of eight birds from Melville Island the white along the inner edge of the primaries starts on primary 4 in the case of five birds, and P. 5 in three. This is a fair sample of the north-western populations. By contrast, in eleven birds from New South Wales it starts on P. 5 and in three on P. 6. Cairns birds are similar, the white starting on P. 5 in ten birds and P. 6 in three. Only three spring adults have been seen from Cape York. In one the white starts on the fourth primary, in one on the fifth, and in the other it becomes pronounced only on P. 6. It starts on the fifth primary in a single spring bird from Russell Island, Torres Strait.

Comparing the breeding race in New Guinea (elisabeth (Heine) 1883) with the birds from eastern Australia Mayr (1937) has written: "The white bar across the wing is usually (but not always) much more pronounced, and starting on the third, instead of the fifth primary." It will thus be seen that the population of *H. macleayi* in north-western Australia approaches the New Guinea type in the wing character.

Melville Island birds are bluer (not so "green-blue") on the back than eastern birds. Occasional individuals are markedly bluer still, the colouring being as rich as in *elisabeth*. These are an October male from South Alligator River (type of Mathews' "distinguendus"), a May male from Palmerston, and an August male from the Margaret River, Wing-length measurements for adult males of *H. macleayi* collected during the breeding season in various parts of the range are: New South Wales (10), 88-96 mm (93); Dawson River (1), 88 mm; Cairns (8), 88-94 mm (92); Cape York (2), 87 and 89 mm; Torres Strait (1), 95 mm; coastal Northern Territory (5), 86-90 mm (88); Melville Island (6), 86-91 mm (88). The differences in wing-length as between the far south and the north-east are reflected in females, nine from New South Wales averaging 93 mm and three from Cape York 87 mm. Mayr, using the same method of measuring as the writer, gives the following measurements for the New Guinea race *elisabeth*: adult males (5), 89-93 mm (91); adult females (5), 88-97 mm (92).

Variation in *H. macleayi* may be summed up by saying that the breeding birds of New Guinea and the north-west of Australia are characterized by a large white wingpatch and blue dorsal colouring and birds from eastern Australia by a small white wingpatch and blue-green colouring on the back. The New Guinea (breeding) birds (*elisabeth*) differ from the north-western ones in tending to be an even richer blue on the back and, apparently, slightly larger.

The two major types of H. macleavi must have arisen in isolation, and there is probably little gene flow between them today. The New Guinea stock is also largely isolated.

From the nomenclatorial viewpoint there is the alternative of recognising only two forms in *H. macleayi* (lumping *elisabeth* under the nominate *macleayi*) or admitting three. The latter is by far the better course, hence the races of *macleayi* will become as follows: *macleayi*, *incincta Gould* 1838, and *elisabeth*. I agree with Mathews that the various additional forms described from the Northern Territory should be sunk into synonymy, *i.e.*, *distinguendus* Mathews 1912, *publa* Mathews 1912, *caeruleus* Ashby 1914. Likewise, there is no basis for *barnardi* Campbell 1911 (Cape York).

Halcyon sancta Vigors and Horsfield 1827. (Sacred Kingfisher.)

This species has almost an Australia-wide range. The habitat is sclerophyll and savannah woodland (especially along streams), and mangroves. It extends seasonally well out into the interior, where there are timbered watercourses. *H. sancta* is rare in Tasmania, being reported only at long intervals in the south (Sharland 1945).

Migration is marked in southern populations, the birds wintering in northern Australia, New Guinea, the Solomons, Bismarcks, and Moluccas. Dates of arrival and departure in the south of the continent are as follows:

Inland New South Wales (Mossgiel)-September and February (Bennett 1909).

Sydney area—end of August or early September and mid-March (North 1909); mid-September and February (Gilbert 1935).

Tasmania (north)—October (Dove 1918).

South-western Australia—first half of September and early March (Serventy and Whittell 1951).

Campbell and White (1910) record migrants striking the lights of ships off the Capricorn Islands in the first half of October. Not all members of *H. sancta* migrate, odd birds being at least as far south as Sydney in the east and in the south-west corner of the continent during winter months.

In the southern parts of the continent migration is regular and birds return to the same valleys and creeks from year to year to breed. In dry parts of the Northern Territory, however, it would appear that they only move into certain areas after the onset of the summer monsoon. Jarman (1944) records this with respect to the Banka Banka area (400 miles north of Alice Springs), the birds arriving with the first rains in December (1942), breeding, and departing again in February. In western New South Wales Bennett states that the length of stay in the area varies with the season.

With regard to dates of arrival at the wintering grounds Mayr (1945) records the birds arriving in the Solomons and Bismarcks during February and March and departing again in September-October. The writer witnessed the arrival of the first migrants at Jacquinot Bay, New Britain, on 18 March 1945. By mid-April the species was dispersed all along the shoreline. The numbers appeared to fall away as early as the end of June. *H. sancta* was a common bird about Port Moresby during the wirter of 1944.

Mayr (1944) has discussed the close relationship of H, sancta to H, australasia of the East Indies, and concludes that the former is but a recent arrival in Australia (as its migratory habits would suggest). It has subsequently invaded New Zealand and the Loyalty Islands from Arstralia, where it has since formed weak races.

Geographic variation: Although there are extensive Australian collections of this species, since it is a migrant only specimens taken during the breeding season can be used in the study of geographic variation. This reduces the amount of material appreciably. Good series of spring-summer birds have been seen from southern Victoria, Sydney and central New South Wales, south Queensland, south-western Australia, reasonably good series from Normanton and Parry's Creek, and smaller numbers from Cairns, Cape York, Carnarvon, Derby and the coastal Northern Territory.

Halcyon sancta is individually a very variable species. This applies particularly to the ventral surface and nuchal collar, in each population individuals ranging from pale buff to deep ochraceous over these areas. To what extent age is involved here is unknown.

There is a suggestion of a geographical sorting-out of *Halcyon sancta* so far as the colour of the nuchal collar and under-surface is concerned. These parts of the body tend towards white in twenty-two out of twenty-five birds from the south-west corner of the continent compared to only twelve out of twenty-six from Victoria (birds in American Museum of Natural History Collection), in each case the rest being of a richer, ochraecous colour. Over the bulk of the continent the more brightly coloured under-surface is dominant. The basis of this colouring requires study. Campbell (1901) created a south-western race (*westralasianus*) on the whitish ventral colouring and Mathews also comments upon the character. A separate race here is unjustified.

Wing-length measurements for adult males, taken during the spring and early summer, from various parts of the range are: Melbourne area (9), 91-98 mm (94); Sydney area (15), 90-98 mm (94); Brisbane-Bunya Mountains (5), 94-100 mm (95); Cairns (3), 93-95 mm (94); Normanton (4), 85-93 mm (90); Cape York (2), 86 and 91 mm; south-western Australia (7), 90-96 mm (93); Derby (4), 90-95 mm (93); Parry's Creek (4), 90-93 mm (92); coastal Northern Territory (2), 90 and 92 mm; Alexandra (1), 92 mm. There is some suggestion that breeding birds from the north of the continent are slightly smaller. The remarks of Keartland (1909) that the eggs of birds from the Fitzroy River are "much smaller" than those from the south should be noted.

Variation in *Halcyon sancta* is of a minor clinal type.

Several races have been described in Australia as follows: *ruficollaris* (Bankier) 1841 (Port Essington); *westralasianus* Campbell 1901 (south-western Australia); *confusus* Mathews 1912 (Cooktown); *ramsayi* Mathews 1912 (Parry's Creek). None of these is justified.

Halcyon chloris (Boddaert) 1783. (Mangrove Kingfisher.)

This kingfisher is strictly an inhabitant of the coastal mangroves and shoreline of the northern half of the continent. Its southern limit in the east is Brisbane and in the west, Carnarvon (Serventy and Whittell). The Australian form extends into New Guinea (Mayr 1941). *H. chloris* is a widespread species, being broken up into some forty races between Africa and the Pacific (Mayr 1945).

In Australia *H. chloris* is a migratory species. It arrives at Cape York from the north at the beginning of September (MacGillivray 1914) and reaches south Queensland at the end of that month (Miller 1936). The birds leave for the north in March but a few over-winter in the south. In the west of the continent Carter (1909) states that *H. chloris* is a common bird at Point Cloates from December until April. A bird was recorded in mid-June, however, and a pair on 1 September. The writer collected a bird at Port Keats (the only one seen) in August 1952.

Geographic variation: Museum material of this species is scanty. Moreover, there is much individual variation.

Specimens seen by the writer from Melville Island, Port Keats and Anson Bay, Cape York, Cooktown (the "type"), Cairns, Bowen, Aru Islands, and Daru, New Guinea, are of the same general type. Each bird in a pair from Point Cloates, near the southern extremity of range, and collected during the winter, has the green of the back much reduced and could best be described as brown above with a greenish tinge on the lower back, wings and rump. To what extent this drab colouring is due to age or seasonal factors cannot be stated. The remarks of Thomson (1935) to the effect that the plumage changes at the time of the moult from a dull sombre green to a vivid colour should be noted.

A pair of birds from Brisbane in the American Museum of Natural History Collection, and five unsexed birds in the Australian Museum, stand apart in having the top of the head green and the whole of the back, wings, and rump a bright blue-green. This contrasts with the dark brownish-green back and more drab blue-green wings and rump of birds from elsewhere. The Brisbane material was all collected in the mid-spring, however, and from no other locality is there an adequate series to compare with it. Wing-length measurements for adult males of H. chloris from various parts of the species' Australian range are: Brisbane (4), 104-110 mm (106); Cairns (1), 110 mm; Cooktown (1), 107 mm; Cape York (3), 104-112 mm (109)—Thomson gives measurements of four November-December males as 105-119 mm (112); Groote Eylandt (2), 100 and 105 mm; Melville Island (3), 102-106 mm (104); Point Cloates (1), 97 mm; Aru Islands (2), 102 and 109 mm; Daru, New Guinea (2), 99 and 106 mm.

More material will be necessary before geographic variation in H. chloris in Australia can be understood. The race described from south Queensland (colcloughi Mathews 1916) may well prove to be justified. The forms cooktowni Mathews 1912 (Cooktown) and melvillensis Mathews 1912 (Melville Island), as the author subsequently admitted, are superfluous.

Tanysiptera sylvia (Gould) 1850. (White-tailed Kingfisher.)

The Australian form of this species is an inhabitant of the tropical rain-forests of the north-east corner from Cape York to Mount Spec, the southern limit also of its breeding range (J. O. Campbell, pers. com.). It winters in south-western New Guinea from the Setekwa to the Fly Rivers (Mayr 1941), arriving at Cape York from the end of October through November, departing again at April (Barnard 1909).

The Australian population of T. sylvia is a distinctive isolate (colour grounds). Winglength measurements of typical adult birds are: Males (9) 95-102 mm (97); females (5) 93-97 mm (95).

VARIATION AND SPECIATION

Geographic forms in the Alcedinidae may be subdivided as follows:

(a) Morphologically-differentiated isolates with the potential of developing into new species:

Dacelo leachii cliftoni (Hamersley region of West Australia) and D. leachii intermediasuperflua (New Guinea); Syma torotoro flavirostris and Tanysiptera sylvia sylvia (isolated Cape York populations of New Guinea species); Alcyone azurea pulchra (Northern Territory probable isolate); Halcyon macleayi macleayi (Northern Territory—probable isolate). There is also a fair measure of isolation between the Australian and New Guinea forms of Alcyone azurea, Halcyon macleayi, Alcyone pusilla (slight gene flow across Torres Strait?).

(b) Former distinctive isolates as indicated by hybrid zones:

Alcyone pusilla halli and A. pusilla ramsayi intergrade from Gulf of Carpentaria to Cape York and there is evidence of some southward gene flow from New Guinea (A. pusilla pusilla) into Cape York. In Halcyon macleayi there would appear to be limited gene flow into Cape York (incincta) from the New Guinea elisabeth.

(c) Former isolate presumed to be connected to parental form by hybrid zone:

Dacelo novaeguineae minor (Cape York),

(d) Isolates that have not yet become differentiated:

The Tasmanian population of *Alcyone azurea* comes into this category and possibly also the Mount Lofty population.

(e) Clinal races (i.e., forms that, in the absence of isolation, are of no immediate evolutionary significance):

(i) South-north clines of decreasing size: These occur in Alcyone azurea, Alcyone pusilla, Dacelo leachii, and possibly in Halcyon macleayi. There is a suggestion of one in Halcyon sancta. Dacelo novaeguineae has a small northern form but it is restricted to Cape York Peninsula. That is to say this species does not vary significantly in size over the bulk of its north-south range (some 1,400 miles) but it does over the last 200 miles. This indicates isolation, past or continuing.

An interesting question is whether or not south north size trends continue across Torres Strait (distributional barrier) in those species that extend to New Guinea. It apparently varies with the species. In A. azurea and A. pusilla the New Guinea individuals would appear to be the same size as the Cape York ones. The New Guinea form of Dacelo leachit, however, appears to be larger than the adjacent mainland one, indicating that under isolation the trend has reversed.

(ii) Colour clines: These are best seen in Dacelo leachii. Populations have darker backs where rainfall is highest; that is, the variation apparently has a climatic basis.

(f) Species in which there is no or negligible geographic variation:

Halcyon pyrrhopygia, the only true interior species, does not vary. Continuity of range and the fact that the nomadism increases the chances of individuals from different parts of the continent mating, are relevant factors here.

Halcyon sancta would appear to have a limited amount of clinal variation, but certainly not sufficient to warrant recognition. The species is apparently a recent immigrant to Australia (Mayr). It undertakes a certain amount of south-north migration.

DISTRIBUTIONAL BARRIERS IN THE KINGFISHERS

These are as follows:

Water Barriers.

(i) Torres Strait (width about 100 miles, but with intervening islands; see Fig. 1). This isolates distinctive forms in several species.

(ii) Bass Strait (width about 120 miles, with some intervening islands). This barrier stops the southward spread of *Dacelo novaeguineae*. The Tasmanian stock of *Alcyone azurea*, isolated to the south of it, has not differentiated. Bass Strait is not of great importance in the kingfishers since they are essentially a tropical group.

(iii) Sea barrier between Melville Island and the adjacent mainland (width perhaps only 10 miles). This could have assisted in the development of the dark Melville population of *Dacelo leachii*. (See Fig. 1.)

Land Barriers (inhospitable terrain).

(i) Tongue of Great Sandy Desert that extends to the sea at Ninety-Mile Beach, northwestern Australia. The distinctive race of *Dacelo leachii* (*cliftoni*) has developed to the south of this (see Fig. 1). The presence of odd "intermediate" birds on the Fitzroy River suggests there may be some crossing of the barrier from the south today.

(ii) Dry country at head of Gulf of Carpentaria. This isolates (or formerly isolated) the distinctive north-western forms of Alcyone azurea, Halcyon macleayi, and A. pusilla.

(iii) Nullabor Plain is a barrier to the westward spread of the Kookaburra, Dacelo novaeguineae. Alcyone azurea reaches no further west than Spencer Gulf. Spread of the latter may be prevented by absence of streams but why D. novaeguineae is absent from the south-west is a major distributional mystery for the majority of eastern forest forms are also in the south-west. Obviously it was an occupant of the south of the continent at the time when good country extended across the head of the Great Australian Bite and forest birds occurred from east to west. Now that it has been artificially introduced to the south-western forests D. novaeguineae is thriving there.

NOMENCLATURE

The following geographic forms should be recognised in the Australian Alcedinidae:

Alcyone azurea azurea Latham 1801. Synonyms: diemenensis and victoria. South Australia to Tasmania and New South Wales, grading into

A. azurea mixta Mathews 1912. Eastern and northern Queensland.

A. azurea pulchra Gould 1846. Synonym: alisteri. Coastal Northern Territory and the Kimberleys.

Alcyone pusilla halli Mathews 1912. Synonym: yorki. Hinchinbrook Island to Cairns, merging via the Cape York and Gulf of Carpentaria populations into

A. pusilla ramsayi North 1912. North-western Australia.

Syma torotoro flavirostris Gould 1850. Northern Cape York.

- Dacelo novaeguineae novaeguineae Hermann 1873. Synonym: tregellasi. Southern Australia north to Cairns.
- D. novaeguineae minor Robinson 1900. Synonyms: mclennani and watsoni. Cooktown to Cape York.
- Dacelo leachii leachii Vigors and Horsfield 1827. Synonyms: macarthuri, occidentalis and mungi. South Queensland, across the inland to the Gulf of Carpentaria, Northern Territory, and Kimberleys.
- D. leachii kempi Mathews 1912. Cape York.
- D. leachii cervina Gould 1838. Synonym: nana. Melville Island and adjacent coast of Northern Territory.
- D. leachii cliftoni Mathews 1912. De Grey River to Shark Bay, Western Australia.
- Halcyon pyrrhopygia Gould 1840. Synonyms: obscurus, utingi. Australia generally, drier regions.
- Halcyon macleayi macleayi Jardine and Selby 1830. Synonyms: distinguendus, publa, caeruleus. North-western Australia.

Halcyon sancta sancta Vigors and Horsfield 1827. Synonyms: ruficollaris, ramsayi, westralasianus, confusus. Australia generally.

Halcyon chloris sordida Gould 1842. Synonyms: cooktowni and melvillensis. Northern shoreline of Australia from Carnarvon in the west to eastern Queensland. Future work may show that the populations of south Queensland belong to a separate race.

H. chloris colcloughi (Mathews) 1916.

Tanysiptera sylvia Gould 1850. Synonym: dydimus. Cape York to Mount Spec.

SUMMARY

A taxonomic study of the Australian kingfishers reveals that out of ten species four do not vary geographically within the continent. Two of these, however, are New Guinea species with a mere toehold in the north-east. Of the other species *Dacelo leachii* is divisible into four races within Australia, whilst Dacelo novaeguineae. Alcyone azurea, A. pusilla. and Halcyon macleayi, have two each.

Isolates (forms with the potential of developing into new species) are few. Five species each have a distinctive form that must have arisen in isolation. In three of these (Dacelo leachii cliftoni, Alcyone azurea pulchra, Haloyon macleayi macleayi) isolation would appear to be still virtually complete. In Alcyone pusilla, however, distinctive north-eastern populations, by a hybrid zone. The small Cape York form of Dacelo novaeguineae (minor) is presumably also now connected with the main stock by a hybrid zone.

Three isolates in ten species means that there is less than one form with the potential of developing into a new species to every three species in the Australian kingfishers. This is a relatively low figure and shows that isolation within Australia is of much less importance than between the continent and New Guinea.

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