# Diversity in the Australian Magpie *Gymnorhina tibicen*: a taxonomic review

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**ABSTRACT** – Diversity among Australian Magpies is most readily recognised by the presence or absence of a black back band or a partial band; there are also differences in tibial and tail plumages. In addition, young birds and adult females of some forms have backs that are extensively black rather than grey, and there is variation in body size, bill size and bill proportion, which is largely clinal. Populations across northern Australia are variable, with narrower and lower-placed back bands; they share traits with magpies on Groote Eylandt and in New Guinea. Divergence in mitochondrial DNA is correlated with variable and subtle phenotypic distinction between western and eastern mainland populations, but extensive genetic and phenotypic intermixing is evident across much of the continent. We propose recognising four subspecies among mainland magpies and three island subspecies in Tasmania, New Guinea and Groote Eylandt, respectively. There is scope for further analysis.

## INTRODUCTION

### Plumage diversity in Australian Magpies

The Australian Magpie *Gymnorhina tibicen* (Latham, 1801) is an Australian icon, a widely distributed and familiar songbird (Schodde and Mason 1999; Higgins *et al.* 2006; Kaplan 2019). Schodde and Mason (1999) recognised nine subspecies in a taxonomic revision that they considered incompletely resolved but which stands to the present (Higgins *et al.* 2006; Menkhorst *et al.* 2017; Gill *et al.* 2023).

The magpie's varied plumage forms prompted early descriptions of several species. The first to be named after *G. tibicen* was *G. hypoleuca* (Gould, 1837), the White-backed Magpie of Tasmania, followed by *G. leuconota* Gould, 1844, the larger white-backed mainland form, then *G. dorsalis* AJ Campbell, 1895, the Varied or Western Magpie of south-western Australia, and *G. longirostris* Milligan, 1903, the Long-billed Magpie of the Pilbara in Western Australia.

Mathews (1912) was the first to recognise subspecies among Australian birds; he named *G. t. terraereginae* Mathews, 1912, a smaller black-backed magpie from Queensland, *G. t. finki* Mathews, 1914 from Central Australia, also long-billed, and other local forms long synonymised. The Official Checklist (RAOU 1926) did not endorse the subspecies concept and recognised only three magpie species, *G. tibicen, G. hypoleuca* and *G. dorsalis*. *G. leuconota* was placed in synonymy with *G. hypoleuca*, and *G. longirostris*, *G. t. terraereginae*, *G. t. finki* and *G. t. eylandtensis* HL White, 1922 of Groote Eylandt, Northern Territory, with *G. tibicen* (Black-backed Magpie). Campbell (1929) proposed including *G. longirostris* as a fourth species, encompassing north-western, northern and central Australia, with *G. t. eylandtensis* and *G. t. finki* in synonymy.

Mathews (1922–1923) and Amadon (1951) retained two species, Black-backed Magpie *G. tibicen* and White-backed Magpie *G. hypoleuca*, but Carrick (1963) combined them while separating *G. dorsalis* specifically. Condon (1951) and Storr (1951) recognised only one species *G. tibicen*, as did Schodde (1975), but others continued to name up to three (Serventy and Whittell 1967; Macdonald 1973; Hall 1974; Burton and Martin 1976; Black and Ford 1982).

A one-species consensus was achieved following Christidis and Boles (1994) and Schodde and Mason (1999), although there was unease about the latter authors' tentative recognition of seven mainland subspecies, two newly named, and extensive zones of intergradation (Figure 1) (Horton 2000; Johnstone and Storr 2004; Higgins *et al.* 2006). The subspecies listed were *hypoleuca* (Tasmania), and on the mainland: *tibicen*, *terraereginae*, *tyrannica* plus *telonocua* (replacing *leuconota*, see Discussion), *dorsalis*, *longirostris* and *eylandtensis*, the last including Kimberley and Northern Territory populations formerly placed ambiguously among black-backed forms or included in *longirostris*. The broad distributions and phenotypic characteristics of all subspecies including New Guinean *papuana* (see below) are summarised in Table 1. Study skins of mainland Australian Magpie subspecies, as well as indeterminate and intergradient specimens, are shown in Figures 2 and 3.

## The New Guinean Magpie

From beyond the Australian land mass, Bangs and Peters (1926) described *Gymnorhina tibicen papuana* from the Trans-Fly region of New Guinea as a subspecies of Black-backed Magpie. They noted that the holotype, an adult female, was larger than Groote Eylandt *G. t. eylandtensis* and shared white tibial plumage with the Long-billed Magpie *G. t. longirostris* of the Pilbara in Western Australia, but with a stouter bill and narrower white nuchal (= nape) patch. Amadon (1951) examined a subadult male, two adult females and a younger male of *papuana*. He found them smaller than *longirostris*, in which he placed Central Australian *G. t. finki* in synonymy while remaining non-committal on the treatment of northern Australian magpies. He regarded the smaller nuchal patch as a valid character but

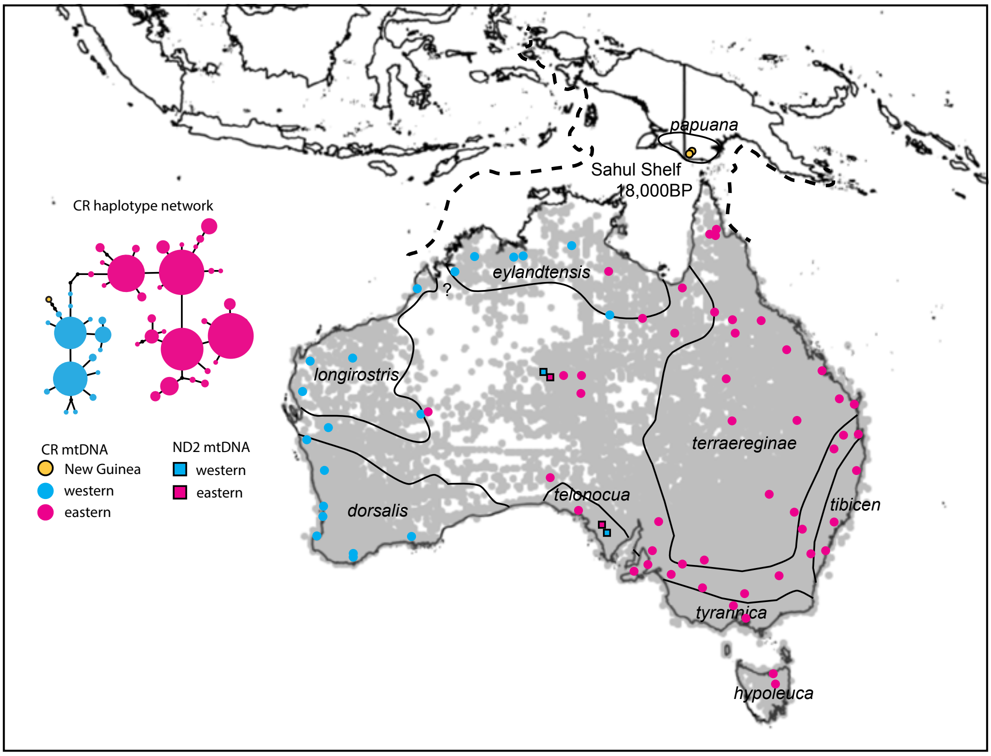

**Figure 1.** Distribution of the Australian Magpie showing records (as grey dots) mapped in the Atlas of Living Australia (https://www.ala.org.au) with subspecies boundaries following Schodde and Mason (1999), the region occupied by magpies in New Guinea, and an outline of the Sahul Shelf that provided their inferred contact with Australian mainland populations. Also shown are the mtDNA haplotype network and haplotype sample sites of Toon *et al.* (2007, 2017) (control region) and the two sample sites of Chesser and ten Have (2001) (ND2) referred to in the text.

**Table 1.** Australian and New Guinean Magpie subspecies, distribution and plumages, after Schodde and Mason 1999 (Black 1986 for *papuana*).

| **Subspecies** | **Distribution** | **Adult male dorsal plumage** | **Adult female dorsal plumage** | **Other characteristics** |
|---|---|---|---|---|
| *terraereginae* | North-eastern and inland eastern Australia | Broad black band on a white back | Similar, grey above and below back band | A small magpie |
| *tibicen* | Sub-coastal eastern Australia | As above | As above | A large magpie |
| *tyrannica* | Southern Victoria and south-eastern South Australia | Fully white back | A mostly grey back with feathers variably tipped white | The largest magpie; broad terminal tail band |
| *hypoleuca* | Tasmania and Furneaux Islands, Bass Strait | Fully white back | A slightly darker grey than *tyrannica* | Smaller than any mainland subspecies |
| *telonocua* | Eyre and Yorke Peninsulas, South Australia | Fully white back | As *hypoleuca* above | A medium sized magpie |
| *dorsalis* | South-western Western Australia | Fully white back | A mostly black back with feathers variably tipped white | A medium sized magpie |
| *longirostris* | Mid-western Western Australia | Variable-width* black band on a white back | Similar, grey above and below back band | A medium-small magpie, long-billed, white tibial plumage |
| *eylandtensis* | Northern Australia, Kimberley to Gulf of Carpentaria | Narrow low-placed black band on a white back | Similar, grey above and below back band | A small magpie, variable tibial plumage |
| *papuana* | Southern New Guinea | Narrow black bar hidden by white back plumage | A mostly black back | The smallest magpie, massive bill, white tibial plumage |

*Black and Ford 1982; Matthew 2006.

doubted the significance of white tibial plumage, which he found variable in *longirostris* and 'probably varies with age'. Mees (1964) described 'the first fully adult male' from New Guinea as white-backed, noting that 'in the white-backed forms the males do not attain an entirely white back until they are several years old.' Mees (1982) published a photograph of that specimen and described an immature male.

Black (1977, 1986) compared all but the holotype among the above New Guinean specimens with Australian representatives and observed that the extensively black dorsal plumage of all but the fully adult male resembled that of female and immature *G. t. dorsalis* of south-western Australia. The narrow white 'nuchal patch' is a consequence in both subspecies of the extensively black back, distinct from the well-defined but restricted black band or saddle of the typical Black-backed Magpie *G. t. tibicen*. The fully adult male, which was assessed as being at least ten years old, unlike *dorsalis* (subspecific epithets used for simplicity hereafter) retained a narrow bar of black feathers on the back that was hidden by long white lower neck feathers. In its long bill, exceptionally large in combined dimensions, and white tibial plumage, *papuana* shared traits also with *longirostris*, as earlier authors had observed (Figure 4).

**Figure 2.** Dorsal view of museum specimens of Australian Magpie *Gymnorhina tibicen* adult males. From left to right, SAMA B5320 Etadunna SA (*terraereginae*), SAMA B55950 Adelaide SA (*tyrannica/telonocua*), SAMA B58182 Langhorne Creek SA (black-backed/ white-backed 'hybrid'), SAMA B24281 Yuendumu NT (northern black-backed).

**Figure 3.** Dorsal view of museum specimens of Australian Magpie *Gymnorhina tibicen* adult females. From left to right, SAMA 55896 Murnpeowie SA (*terraereginae*), SAMA B55933 Cungena SA (*telonocua*), SAMA B17606 Bridgetown WA (*dorsalis*), SAMA B16647 Beechborough WA (*dorsalis*).

## Genetic aspects

In a phylogeographic study of the Australian Magpie, Hughes *et al.* (2001) sequenced the mitochondrial control region of 868 individuals of 17 populations from the south-western and eastern mainland and Tasmania. They detected no correlation between back colour and haplotype but showed that haplotype divergence was greatest between south-western and all eastern populations. With an increased sample of 1166 and greater geographic cover, including northern and north-western Australia, Toon *et al.* (2003, 2007) identified two mtDNA (control region) phylogroups distributed east and west across Australia without overlap (Figure 1). Toon *et al.* (2007) showed a similar eastern and western division in nuclear DNA but with eastern microsatellite alleles present in western mtDNA haplogroup Kimberley and Pilbara samples; they attributed this mito-nuclear discordance (Rheindt and Edwards 2011; Toews and Brelsford 2012) to secondary contact between northern populations. Earlier distinction between black-backed and white-backed forms of northern and southern disposition respectively found no support from any of these studies. Hughes (1982), Hughes *et al.* (2001, 2002, 2011) and Dobson *et al.* (2019) treated the presence or absence of a black back band as a variable morph, heritable and probably polygenic, but its selective basis remained elusive (Hughes *et al.* 2002). Toon *et al.* (2017) sequenced mtDNA from three recently acquired specimens of *papuana* and showed that the New Guinean subspecies is sister to the western mtDNA phylogroup comprising *dorsalis*, *longirostris* and western representatives (Toon *et al.* 2007) of *eylandtensis* (Figure 1). Those three fully adult males had well defined back bands and thus differed from all previously described or illustrated examples of the subspecies (Figure 5). Toon *et al*. (2017) questioned whether adult males of *papuana* are polymorphic with respect to back band width or if the extent of black diminished with age in males, unlike typical Black-backed Magpies in which band width remains unchanged throughout life (Cole 1921; Black and Ford 1982; JH unpublished; Schodde and Mason 1999; Dobson *et al.* 2019).

While it is clear that *papuana* shares traits with and is genetically closer to both *dorsalis* and *longirostris* than to geographically closer *terraereginae* of central Cape York Peninsula, its affinity with *eylandtensis*, a potentially contiguous population across the dry-land Sahul Shelf connecting New Guinea and Australia before its Holocene inundation (Toon *et al.* 2017), has not been addressed (Figure 1). Toon *et al.* (2017) urged reassessment of *eylandtensis* (*sensu* Schodde and Mason 1999), observing that it included some magpies with eastern mtDNA haplotypes and others with western ones.

Here we compare the plumage diversity now revealed among New Guinean magpie specimens with presently recognised Australian forms, and with *eylandtensis* in particular.

From a synthesis of the above information, we summarise geographic variation within *Gymnorhina tibicen* in a review of its infraspecific taxonomy. We address the following:

1. whether available phenotypic, genetic and distributional data support recognition of all currently named subspecies (*sensu* Schodde and Mason 1999), consistent with recent application of that taxonomic rank;

2. whether the three mtDNA haplogroups (Toon *et al.* 2017) might provide a practical basis for revision; thus, eastern Australian, western Australian and New Guinean magpies; and

3. whether to regard the Australian Magpie's varied plumage forms simply as morphs within a monotypic species (Hughes 1982; Hughes *et al.* 2001, 2003, 2011; Dobson *et al.* 2019).

## METHODS

We reviewed descriptive details of all known *papuana* specimens (Black 1986; Toon *et al.* 2017). We collated available morphometric and plumage data for all Australian subspecies and some intergradient populations from the following sources: Black and Ford (1982); Black (1986); Schodde and Mason (1999); Johnstone and Storr (2004, western populations only); and Matthew (2006). Most sources gave mean figures and standard deviations for each measurement; a mid-point in the stated range of Schodde and Mason (1999) was applied for comparative purposes. Metrics included bill size as bill length (exposed culmen from skull base to tip) and wing length as flattened chord. Bill relative size, as bill/wing ratio, was reported or calculated from all sources. All but one source provided the width of the black terminal tail band and all but one provided tail length. Overall length and tarsus length were not consistently represented and are not included in this review.

**Figure 4.** Dorsal view of *Gymnorhina tibicen papuana* (from Black 1986, image B Popowycz). From left to right, RMNH 30137 adult male, RMNH 33673 subadult male, AMNH 427517 adult female, AMNH 422198 juvenile male.

**Figure 5.** Dorsal view of *Gymnorhina tibicen papuana*. From left to right, ANWC 56205, ANWC 56302, ANWC 56218, all adult males. Image L Joseph

Also noted were the presence, breadth and other attributes of any black back band, tibial plumage (black, white or mixed), tail band width, and melanism (increased black pigmentation) as described in the back plumage of young birds and adult females of subspecies *dorsalis* and *papuana*.

As part of our review of northern populations assigned to subspecies *eylandtensis*, one of us (AB) examined the syntype series and reviewed plumage and other information on all known specimens from Groote Eylandt.

We reviewed all available genetic data and one of us (AT) sequenced five additional museum specimens from the Australian National Wildlife Collection (ANWC) for the mtDNA control region, as described by Toon *et al.* (2017). Sequences were edited and aligned with previous datasets and mapped to their sampling locations.

## RESULTS

### New Guinean specimens

Morphometric and plumage traits of all ten known specimens of subspecies *papuana* are summarised in Table 2: the holotype female (Bangs and Peters 1926), the four males and two females examined by Black (1986) and the three

**Table 2.** Measurements in mm and plumage traits of ten *papuana* specimens, listed for simplicity as M1–7 (males) and F1–3 (females). ANWC data are from L Joseph, otherwise all are from Black (1986), with other authors in square brackets: Bangs and Peters (1926, F1), Amadon (1951, M3, F1, F2, F3, bill length only) and Mees (1964, M1; 1982, M2). Acronyms are: AMNH = American Museum of Natural History, New York, NY, USA; ANWC = Australian National Wildlife Collection, Canberra; MCZ = Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts, USA; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands.

| Specimen | Bill | Wing | Tail band | Tail shafts | Back pattern | Notes |
|---|---|---|---|---|---|---|
| M1 RMNH 30137 | 68 [67.5] | 250 [246] | 45 | White | White back with concealed narrow black band | Old male |
| M2 RMNH 33673 | 63 [62] | 240 [240] | 70 | Black | Mostly black | 2nd (or 3rd) year |
| M3 AMNH 427516 | 64 [64] | 230 | 50 | Black | Mostly black | 2nd (or 3rd) year |
| M4 AMNH 422198 | 56 | 232 | 85 | Black | Mostly black | Juvenile |
| M5 ANWC 56205 | 62 | 237 | 55 | Black ± white | Low-placed back band of reduced width | Adult male |
| M6 ANWC 56302 | 67.5 | 234 | 60 | White ± black | As for M5 | Adult male |
| M7 ANWC 56218 | 65 | 244 | 45 | White ± black | As for M5 | Adult male |
| **Adult male mean** | **64.9** | **239.2** | **54.2** | | | **Bill/wing ratio = 0.271** |
| F1 MCZ 99653 | [63] [64] | [245] | [60] | Not described | Black-backed with narrow 'nuchal patch' | Adult female |
| F2 AMNH 427517 | 61 [60] | 228 | 60 | Black | Mostly black | Adult female |
| F3 AMNH 422199 | 62 [62] | 228 | 50 | Black | Mostly black | Adult female |
| **Adult female mean** | **62.0** | **233.7** | **56.7** | | | **Bill/wing ratio = 0.265** |

recently collected males (Toon *et al.* 2017); dorsal plumage variation is shown in Figures 4 and 5.

M1 is the adult male described and illustrated by Mees (1964, 1982) as a fully white-backed individual, but it retains a narrow bar of black feathers concealed by overlying white feathers of the mantle (Black 1986). It is an old male, as shown by fully white shafts to the white portion of its rectrices (Robinson 1956; Black 1986; Matthew 2006).

M2 has many feathers of the underparts mottled brown-grey (AB unpublished data 1975–77); described as immature by Mees (1982), it is presumably in its second or third year.

M3 has a grey-brown throat and grey-brown tips to black leg feathers (AB unpublished data 1975–77); described as subadult by Amadon (1951), it may be undergoing its second or third moult.

M4 has grey-brown plumage and a small all-dark bill (AB unpublished data 1975–77) and is presumably in its first year.

M5, M6 and M7 have adult plumages with the shafts of rectrices in stages of whitening, with M6 and M7 more advanced. Their low-placed black back bands are narrower than those of *tibicen* and *terraereginae* and white traces are present in some black back feathers (Figure 5).

F1, the adult female holotype, has not been examined personally. F2 and F3 have adult plumages (AB unpublished data 1975–77).

All specimens have white tibial plumage.

## Australian specimens

The following data are collated from the sources listed in Methods, of which Matthew (2006) is the most comprehensive and has the most extensively analysed statistical data. Male metrics are presented, in view of their mostly larger samples. Female measurements were generally smaller, with statistically significant sexual dimorphism in most subspecies in wing length ($p < 0.01$) and in all subspecies in bill length ($p < 0.05$) (Matthew 2006).

**Table 3.** Morphometrics (mm, mean or mid-point of range) of adult males in subspecies of the eastern phylogroup, generally from north to south. Data are from Matthew (2006) with comparable groups from Black (1986) shown as AB, and figures from Schodde and Mason (1999) shown as S&M. Numbers in brackets are maximum sample sizes for each group. Further data can be found in source references.

| Taxon or population (n) | Bill | Wing | Bill/wing ratio | Tail | Tail band |
|---|---|---|---|---|---|
| *terraereginae* (29) | 55.2 | 250.0 | 0.221 | 135.0 | 40.6 |
| “ AB (17) | 52.0 | 249.0 | 0.209 | 135.0 | |
| “ S&M | 53.0 | 255.0 | 0.208 | | |
| *tibicen* (7) | 54.8 | 270.7 | 0.202 | 142.1 | 47.8 |
| “ AB (34) | 53.0 | 269.0 | 0.197 | 153.0 | |
| “ S&M | 51.5 | 272.5 | 0.189 | | |
| *tyrannica* (27) | 56.4 | 277.1 | 0.203 | 144.8 | 70.9 |
| ″ S&M | 54.5 | 280.0 | 0.195 | | |
| *tyrannica* x *telonocua* (16) | 58.1 | 266.6 | 0.217 | 140.9 | 67.0 |
| “ “ “ AB (17) | 55.0 | 269.0 | 0.204 | 141.0 | |
| *telonocua* (8) | 56.5 | 251.8 | 0.224 | 135.9 | 57.0 |
| “ S&M | 53.0 | 260.0 | 0.204 | | |
| *hypoleuca* (14) | 49.1 | 251.2 | 0.195 | 138.0 | 58.7 |
| “ S&M | 45.0 | 253.0 | 0.178 | | |

**Table 4.** Morphometrics (mm, mean or mid-point of range) of adult males in populations of the western phylogroup, from north to south. Data are from Matthew (2006), and Johnstone and Storr (2004) as J&S, with some comparable groups plus *papuana* from Black (1986) and Table 2, shown as AB, and figures from Schodde and Mason (1999) as S&M. Numbers in brackets are maximum sample sizes for each group. Further data can be found in source references.

| Population (n) | Bill | Wing | Bill/wing ratio | Tail | Tail band |
|---|---|---|---|---|---|
| *eylandtensis* (9) | 60.9 | 246.7 | 0.247 | 136.1 | 32.0 |
| “ S&M | 59.0 | 242.5 | 0.243 | | |
| Kimberley J&S (17) | 60.7 | 245.4 | 0.247 | 134.9 | |
| *eylandtensis* plus *longirostris* AB (9) | 61.0 | 249.0 | 0.245 | 135.0 | |
| *longirostris* (6) | 64.4 | 244.6 | 0.263 | ? | 38.2 |
| “ S&M | 62.5 | 252.5 | 0.248 | | |
| Pilbara J&S (31) | 64.4 | 251.9 | 0.256 | 135.8 | |
| Gascoyne/Murchison J&S (28) | 59.8 | 252.6 | 0.237 | 137.0 | |
| *longirostris-dorsalis* intergrades J&S (75) | 59.7 | 254.3 | 0.235 | 137.1 | |
| *dorsalis* (19) | 59.9 | 259.6 | 0.231 | 136.5 | 35.5 |
| “ J&S (185) | 59.3 | 262.3 | 0.226 | 138.8 | |
| “ AB (23) | 58.0 | 260.0 | 0.223 | 135.0 | |
| “ S&M | 58.0 | 264.0 | 0.220 | | |
| *papuana* AB (6) | 64.9 | 239.2 | 0.271 | 126.0 | 54.2 |

Tables 3 and 4 are based on the findings of Matthew (2006) and Table 4 includes the larger western samples of Johnstone and Storr (2004), who grouped five successive latitudinal populations: Kimberley (= *eylandtensis*); Pilbara; Gascoyne/Murchison (both = *longirostris*); *longirostris* x *dorsalis* intergrades; and *dorsalis*. Measurements for *papuana* are from Table 2 and Black (1986).

Morphometric data from the separate sources are broadly consistent, the greatest variation being in bill length measurement, but Johnstone and Storr (2004) and Matthew (2006) were in close agreement also in that parameter.

The broad and well delineated back band is characteristic of subspecies *terraereginae* and *tibicen*. In *longirostris* its width appears to be less consistent (Black and Ford 1982; Matthew 2006) and in *eylandtensis* it is narrower and placed lower (Schodde and Mason 1999; Matthew 2006; JH pers. obs.; AB unpublished data 1974–78). The other kind of black back is found in the immature and adult females of subspecies *dorsalis* and *papuana* and is due to increased pigmentation in back feathers (Black and Ford 1982), a form of partial melanism (van Grouw 2021). White tibial plumage is characteristic of *papuana* and *longirostris* and is present in some *eylandtensis*. The width of the terminal tail band was measured differently by different researchers but with comparable findings; it shows a north-to-south linear increase in eastern populations between *terraereginae* and *tyrannica* ($p < 0.01$, Matthew 2006); it is narrower and relatively unvarying in western populations but broad in *papuana* (Tables 3 and 4).

Latitudes and longitudes of places named in the text are provided in the Gazetteer.

## Groote Eylandt specimens

Only ten specimens of subspecies *eylandtensis* are known from Groote Eylandt: the four syntypes taken in May 1921 by W McLennan (White 1922) in the HL White collection of Museums Victoria (HLW), two in the South Australian Museum, Adelaide (SAMA) taken in January 1922 by N Tindale, two juveniles in the Natural History Museum, Tring, taken by GH (later Sir Hubert) Wilkins in February and March 1925, and an adult male and adult female taken by HG Deignan on the Smithsonian Expedition to Arnhem Land in May and June 1948. The

**Table 5.** Measurements (mm) of *eylandtensis* specimens from Groote Eylandt. Smithsonian Institution (USNM) data are provided by C Milensky, others by AB, with those of White (1922) in square brackets.

| Collection | Specimen | Bill | Wing | Bill/wing ratio | Tail | Tail band |
|---|---|---|---|---|---|---|
| HLW | 5165 adult male | 59.6<br>[57] | 229<br>[224] | 0.260 | 129<br>[145] | 30 |
| HLW | 5163 adult female | 54.5<br>[53] | 220<br>[220] | 0.248 | 126<br>[145] | 40 |
| HLW | 5162 subadult male | 56.4<br>[57] | 226<br>[222] | 0.250 | 127<br>[140] | 50 |
| HLW | 5164 subadult male | 58.0<br>[59] | 230<br>[232] | 0.252 | 130<br>[148] | 40 |
| SAMA | B4088 adult male | 60.8 | 215 | 0.283 | 127 | 35 |
| SAMA | B4089 adult female | 47.3 | 205 | 0.231 | 126 | 45 |
| USNM | 405995 adult male | 62 | 238 | 0.261 | 125 | c. 30 AB |
| USNM | 405996 adult female | 53 | 222 | 0.239 | 120 | c. 35 AB |
| | **Mean male (5)** | **59.4** | **228** | **0.261** | **128** | **c. 37** |
| | **Mean female (3)** | **51.6** | **216** | **0.239** | **124** | **c. 40** |

**Figure 6.** Dorsal view of type series of *Gymnorhina tibicen eylandtensis*. From left to right, NMV HLW 5165 adult male, NMV HLW 5163 adult female, NMV HLW 5162 subadult male, NMV HLW 5164 subadult male. Image K Clarke

findings in eight non-juvenile specimens are summarised in Table 5.

The adult male HLW 5165 is old with pure white shafts to rectrices and exhibits the extensively white hind neck and low, narrow (4 cm) back band that characterise the subspecies (Schodde and Mason 1999). The adult female HLW 5163 has a narrow white nape, below which are black-centred, broadly white-tipped, dark grey feathers above a similarly narrow black back band. Its short bill is damaged at its tip. The subadult males HLW 5162 and 5164 have extensive blackish dorsal plumage below a narrow whitish to pale grey nape. Subtle demarcation between broadly pale-tipped black on grey feathers above and narrowly tipped black feathers below evidently defines the developing black band of maturity (Figure 6). Tibial plumage in each is white with some black flecking.

SAMA B4088 is an adult male with black and white shafts in the rectrices. The specimen is discoloured, and feet described as black are now pale grey; it may have been straightened and foreshortened in preparation. Unlike the older syntype male, it has a narrow whitish nape below which hindneck and mantle feathers are grey with blackish centres. The back band appears to be of average width (6 cm) for a black-backed magpie of this size. Tibial plumage is hidden among belly feathers but appears to be dark. SAMA B4089 is a female, similarly straight, short and discoloured, perhaps from time in preservative, the plumage of its underparts being soft and sooty grey. It has a narrow white nape, an evenly grey hindneck and mantle and a 6 cm width back band. The very short bill is extensively whitened, and its small bill size is thus not explained by immaturity. Furthermore, the shafts of its rectrices are white, an uncommon finding in females, suggesting that this individual is old. Tibial plumage is also hidden.

The Smithsonian Institution specimens are both adult, contrary to Amadon's (1951) view that only the male was adult, and are in fact old, the male (USNM 405995) with all-white shafts to rectrices and the female (USNM 405996) with partially whitened shafts. The pair closely resemble the two syntype adults but have slightly broader back bands (Figure 7). Tibial plumage is mottled. The tail band is narrow, as estimated by AB (Table 5).

The two Natural History Museum specimens (NHMUK 1925.11.1.355 and NHMUK 1925.11.1.998) were examined earlier and both found to be juvenile with mottled grey or brown underparts (AB unpublished data 1974–78). Recent photographs taken by H van Grouw show that each has a narrow white nape patch, with an untidy mix of black or partially black feathers on the upper back, merging with an ill-defined black band above a dark grey rump (Figure 7). Tibial plumage is obscured.

### DNA sequences of additional Australian specimens

Four of the mtDNA control region sequences matched those collected in previous studies

**Figure 7.** Dorsal view of *Gymnorhina tibicen eylandtensis*. From left to right, USNM 405995 adult male, USNM 405996 adult female (image C Milensky), NHMUK 1925.11.1.355, juvenile and NHMUK 1925.11.1.998, juvenile (image H van Grouw).

and one sequence was novel. Sequences have Genbank accession numbers PP098252 to PP098256. Of the five samples, two from near Lake Carnegie, south of the Little Sandy Desert in Western Australia, proved of interest, one with an eastern mtDNA haplotype (ANWC 32973), the other with a western mtDNA haplotype (ANWC 32974) (Figure 1).

## DISCUSSION

### The *papuana* phenotype

The New Guinean Magpie is small (mean male wing length 239 mm), compared with Australian populations (245 to 277 mm). It was thought to be a Black-backed Magpie, close to *tibicen* and especially *longirostris* (Bangs and Peters 1926; Amadon 1951) until Mees (1964) described a white-backed male. Black (1986) found its phenotype closer to western forms *dorsalis* and *longirostris* but magpies illustrated by Toon *et al.* (2017) more closely matched black-backed subspecies *tibicen* and *terraereginae* and especially *longirostris* and *eylandtensis* (Figures 4 and 5). Female, subadult male and juvenile *papuana* specimens resemble *dorsalis* and both subspecies can be recognised as exhibiting melanism in dorsal plumage, perhaps as a retained ancestral character (Black 1986). While three fully adult males (Toon *et al.* 2017) bear a resemblance to *tibicen* or *terraereginae*, their back bands are placed lower and are of reduced width (estimated by JH as 2/4 in the scale of Hughes *et al.* 2011), as described for *eylandtensis* (Schodde and Mason 1999). The very old male (Mees 1964) has an even narrower and almost hidden back band (Black 1986). Evidence is insufficient to conclude whether such variation represents polymorphism in that character or progressive change with age. While the black back band or saddle retains its breadth with age in *tibicen* and *terraereginae*, its genetic basis in those eastern subspecies with higher-placed back bands will not necessarily apply in *papuana*, the sister lineage to the western mtDNA phylogroup. It is plausible that males of the dorsally melanistic subspecies *papuana* exceptionally undergo a progressive loss of black back plumage over an extended period.

### Groote Eylandt and subspecies *eylandtensis*

The northern Australian magpie presently named *eylandtensis* is small with a mean wing length of 247 mm, similar to those of *terraereginae* (250 mm) and *longirostris* (245 mm) (Matthew 2006) with both of which it intergrades (Schodde and Mason 1999). It has a relatively long bill with a male bill/wing ratio of 0.25, intermediate between that of *terraereginae* (0.22) and *longirostris* (0.26) (Matthew 2006; Tables 3 and 4). It includes individuals in the eastern mtDNA phylogroup (with *terraereginae*) and others in the western phylogroup (with *longirostris*) (Toon *et al.* 2007) (Figure 1). It has a narrow and low-placed back band; tibial plumage may be white, black or mixed (Schodde and Mason 1999).

Only eight non-juvenile specimens are known from Groote Eylandt, its type locality (White 1922). Magpies are moderately common on the island which lies about 50 km from the coast south-east of Arnhem Land and marks their approximate northern limit in the Northern Territory (Noske and Brennan 2002; R Noske pers. comm.) (apparent exceptions shown in Figure 1 require corroboration). We confirm Schodde and Mason (1999) and Matthew (2006) in finding that this island population is disjunctly smaller than mainland *eylandtensis* and is the smallest of any Australian Magpie, with a male mean wing length of 228 mm, shorter even than *papuana* (239 mm). We corroborate White's (1922) description of a narrow tail band, as in mainland *eylandtensis* (Schodde and Mason 1999), and long bill in males whose bill/wing ratio of 0.26 approximates that of *longirostris* (Tables 4 and 5).

The dorsal plumage of adult females and subadults of the Groote Eylandt population provides evidence of partial melanism, as in *dorsalis* and *papuana*. Its back band is apparently of average or reduced width and placed low as in *papuana*, whose back band also varies in width. Sexual dimorphism in body size and especially bill size appears from available material to be pronounced.

### Do western and eastern mtDNA phylogroups define taxonomic units?

Toon *et al.* (2003, 2007) established distinct western and eastern mtDNA (control region) phylogroups whose distributions approached closely. At no locality were mtDNA haplotypes from both clades represented although marginal longitudinal overlapping was present in the north within subspecies *eylandtensis* (Figure 1). Nuclear genetic groupings using microsatellites were largely concordant with this pattern and a recent nuclear study using Single Nucleotide Polymorphisms (SNPs) found the same two eastern and western genetic groups and a third genetic cluster from Tasmania (McIntyre 2022), although the sampling of mainland magpies was limited to south-eastern and south-western populations. In the north, Toon *et al.*'s (2007) microsatellite data showed eastern nuclear alleles among western mtDNA phylogroup populations of *longirostris* and *eylandtensis*, confirming secondary contact and extensive intermixing across northern Australia. In southern Australia eastern mtDNA haplotypes extended to Eyre Peninsula and western haplotypes to Esperance in Western Australia, while Eyre Peninsula nuclear data were ambiguous. In an earlier phylogeographic overview of the family Cracticidae on the other hand, Chesser and ten Have (2001) identified western and eastern mtDNA haplotypes (ND2) in both Central Australian and Eyre Peninsula samples. We here provide a further example of the occurrence of both eastern and western mtDNA haplotypes near Lake Carnegie at the southern edge of the Little Sandy Desert in Western Australia (Figure 1).

Although Toon *et al.* (2007) found no congruence between plumage variation and haplotype distribution, populations in the western mtDNA phylogroup, i.e., *dorsalis* and *longirostris* and its sister taxon *papuana*, exhibit some traits that differ from those of the eastern phylogroup, i.e. *terraereginae, tibicen, tyrannica* and *hypoleuca*.

Melanism is evident in the dorsal plumage of adult females and young of *dorsalis*, *papuana* and Groote Eylandt *eylandtensis* but not in mainland *eylandtensis* or *longirostris* or in eastern mtDNA phylogroup members.

White tibial plumage is present in *longirostris* and *papuana* and variably in *eylandtensis* (including Groote Eylandt magpies) but not in *dorsalis* or in eastern magpies.

Western forms generally have larger bills, most notably in *papuana* and Pilbara *longirostris* but comparatively so in all measured groups; the smallest western mean bill/wing ratio (in *dorsalis*, 0.23) exceeds the highest figures in the east (*telonocua* and *terraereginae*, 0.22).

Western forms are slightly smaller overall at equivalent latitudes. Wing lengths increase from north to south in the west from c. 245 to 260 mm and in eastern populations from c. 250 to 280 mm.

Tail bands are broader in eastern than western populations but are of intermediate width in *papuana* (Tables 2 and 3). Campbell (1929) found variation in the extension of black of the tail band along the outer vane of the outermost rectrix and Black (1986) found it greater among eastern than western populations and even more restricted in *papuana*.

However, none of the phenotypic distinctions between western and eastern magpies identified above is discretely partitioned. Variation appears to be clinal across northern Australia within subspecies *eylandtensis* as well as between western and central Australia through the Gibson, Little Sandy and Great Victoria Deserts (Black and Ford 1982; Black 1986; Johnstone and Storr 2004; Figure 1, *pace* Schodde and Mason 1999) and south of the Nullarbor Plain (Black 1975, *pace* Ford 1969), linking south-western *dorsalis* and Eyre Peninsula *telonocua*. The continuity of magpie populations at these three latitudes includes representatives of western and eastern mtDNA haplogroups.

## The significance of a black back band

An obvious early distinction between different magpie populations is the presence or absence of a black back band or saddle but this character is of uncertain significance in evolutionary terms and might result from a trivial genetic mechanism involving relatively few genes, with the white-backed form representing the homozygous recessive state (Hughes 1982; Hughes *et al.* 2001, 2011; Dobson *et al.* 2019).

A pointer against the importance of back colour in separating subspecies, which by definition are restricted geographically (Winker 2010; Patten and Remsen 2017), is the occurrence of white-backed magpies among black-backed populations, perhaps the offspring of heterozygous individuals. This was recognised early in Central Australia, where Hill (1913) and White (in Mathews 1922–1923) reported both forms. The prevailing mix there includes white-backed among narrowly black-backed magpies (Campbell 1929; Cleland 1931, 1932, 1933; Condon 1951; Parker 1969; Hughes and Mather 1980; Black and Ford 1982); this population was given subspecific recognition as *G. t. finki* by Mathews (1914, 1922–23; Condon 1951; Ford 1969; Black 1986). Farther north, Hill (1913) reported a white-backed magpie on the McArthur River in north-eastern Northern Territory (see also Walters 1979; Hughes and Mather 1980), and white-backed magpies and magpies with narrow back bands have been seen in the Kimberley (Toon *et al.* 2017), inland Western Australia (Whitlock in Mathews 1922–1923; Black and Ford 1982), the eastern Great Victoria Desert (Black and Badman 1986), and in north-western and north-eastern South Australia

(Black 1975). These exceptions occur chiefly among what are intergradient populations or those with narrow back bands (Schodde and Mason 1999). Yet there are some from within core black-backed magpie territory, e.g. in north-eastern New South Wales (Campbell 1929) and central and south-eastern Queensland (Hughes and Mather 1980), and Mathews's holotype specimen of *terraereginae* from Mount Bartle Frere in northern Queensland has a reduced back band, if correctly figured in Plate 483 (Mathews 1922–23).

**How many subspecies?**

The place of the subspecies as a taxonomic rank was addressed in 14 papers by North American ornithologists and published in *Ornithological Monographs* in 2010. Subspecies are 'discrete diagnosable geographic populations' (Remsen 2010) within the species that will intergrade if they abut and may be identified at various stages of differentiation along a biological continuum during the process of speciation (Winker 2010). Earlier, Patten and Unitt (2002) emphasised that average measurement differences between populations was not enough to distinguish subspecies, unless they are diagnosable. More recently, Donald (2021) showed that clinal variation is ubiquitous among birds, and that mean differences, no matter the level of statistical significance, may be taxonomically uninformative if the effect of clinal variation is not recognised and accounted for.

We follow Remsen (2010), Winker (2010), Patten and Remsen (2017) and Donald (2021) and suggest that the following criteria be addressed in recognising subspecies in a polymorphic species.

1. Phenotypic variation is partitioned geographically; each subspecies has identified distributional limits.

2. Continuous clinal variation across a population's range represents intra-taxon diversity but steep clines between populations may define subspecies boundaries.

3. Subspecies are diagnosable; while some ambiguity is allowed and its degree is contended, members of a subspecies are generally distinguishable from those of adjacent subspecies.

4. There should be at least one diagnostic trait or a diagnostic combination of independent distinguishing traits.

5. Distinguishing traits including DNA sequences when available, whether separated absolutely or by steep clinal change, are geographically concordant at the proposed subspecies boundary.

Present infraspecific taxonomy of the Australian Magpie (Higgins *et al.* 2006; Menkhorst *et al.* 2017; Gill *et al.* 2023) follows Schodde and Mason (1999) who recognised seven mainland and two island subspecies but were undecided whether extensive and largely unstudied intergradation on the mainland resulted from secondary contact between differentiated isolates. They made two novel proposals.

First, among mainland white-backed magpies they showed that the Victorian (eastern) form is larger than southern South Australian magpies, has an exceptionally broad terminal tail band and its females have paler backs. They named it as subspecies *tyrannica* and showed that it intergraded with the western form of the Eyre and Yorke Peninsulas in South Australia, which they named *telonocua*.

Second was their approach to resolving the unsatisfactory treatment of variable northern Australian populations (Black and Ford 1982; Black 1986) that had been included either in subspecies *longirostris* (Campbell 1929; Condon 1951) or more broadly among *tibicen* (Storr 1967, 1980, 1984; Serventy and Whittell 1967), or overlooked (Amadon 1951). They observed that northern black-backed magpie populations had the appearance of a 'clinally varying mega-subspecies' but that plumages of those in the north and north-west resembled Groote Eylandt *eylandtensis* and so included them tentatively in that subspecies.

Clinal variation among mainland populations includes a north to south increase in wing, tail and tarsus length and decrease in bill/wing ratio in the east, assessed as a simple linear regression ($p < 0.01$, Matthew 2006), a south-trending increase in wing length and decrease in bill/wing ratio in the west ($p < 0.01$) and similar variation in mid longitudes (Matthew 2006). Johnstone and Storr (2004) corroborated many of those trends in western populations across five latitudinal groupings, unrelated to subspecies boundaries (Table 4) but showed that the longest bill is in Pilbara *longirostris* and the next in length is western *eylandtensis*, followed by southern populations of *longirostris*, *longirostris* x *dorsalis* intergrades and *dorsalis*.

Turning to individual subspecies, we observe that ***terraereginae*** increases in size clinally from north to south and is distinguished from ***tibicen*** only in the latter's larger size at equivalent latitudes, with intergradation described as rather abrupt (Schodde and Mason 1999); this has not been analysed statistically.

While subspecies ***tyrannica*** is larger than ***telonocua*** with a wider tail band and its females' grey backs are paler, it is unclear if variation in these parameters is geographically coincident (Black 1986; Schodde and Mason 1999; Hughes *et al.* 2002; this study). Schodde and Mason (1999: 549) suppressed subspecies *leuconota* because its holotype is 'from an intergradient population' in the 'region of Adelaide and Mt Lofty Range'. The genetic and taxonomic status of *telonocua* is ambiguous (see above; Chesser and ten Have 2001; Matthew 2006; Toon *et al.* 2007).

Subspecies ***dorsalis*** is distinguished from all other Australian subspecies by its extensively black-backed females and young males. Unlike eastern magpies, it does not form nonterritorial flocks (Robinson 1956; Hughes *et al.* 2003). Its contact with *telonocua* appears on available evidence to be characterised by extensive clinal intergradation (Black 1975; Black and Ford 1982; Johnstone and Storr 2004; JH pers. obs.; *pace* Ford 1969) and its interaction with *longirostris* (Ford 1969; Johnstone and Storr 2004) has not been analysed in detail.

Subspecies ***longirostris*** has white tibial plumage, perhaps inconsistently (Johnstone and Storr 2004; Matthew 2006), and a longer bill than other mainland forms but only in the Pilbara (Johnstone and Storr 2004). Other magpies assigned to this subspecies in the Gascoyne and Murchison Districts are not so long-billed, and relatively long-billed magpies extend to Central Australia (Hall 1974; Black and Ford 1982) and have been included in *longirostris* (Campbell 1929; Amadon 1951) or as subspecies *finki* (Mathews 1914; Condon 1951; Ford 1969; Black 1986). There is variation in the width of the back band in *longirostris* (Black and Ford 1982; Matthew 2006). Among Western Australian authors, only Ford (1969) recognised this taxon, but not Storr (1967, 1980, 1984), Serventy and Whittell (1967) or Johnstone and Storr (2004) and there is inconsistency in its diagnosis and presumptive range. It shares nuclear alleles with eastern birds (Toon *et al*. 2007), perhaps the result of population and range expansion of the eastern mtDNA phylogroup across northern and central Australia; such gene flow might account for its black-backed plumage and absence of the partial melanism that characterises *dorsalis* and *papuana*.

Burton and Martin (1976) analysed interaction between eastern black-backed (*terraereginae-tibicen*) and white-backed (*tyrannica*) magpies in relation to a single character, the back band. The 30–90 km 'hybrid zone' and 200–300 km overlap (Burton and Martin 1976; Hughes *et al.* 2011) are well known and are loosely correlated with body size but with no other parameter (T Burton *in litt.* to AB January 1975).

Northern populations included in subspecies ***eylandtensis*** are small and relatively long-billed with a narrow and low-placed back band; tibial plumage varies and there is broad intergradation with *longirostris* and *terrarereginae* (Schodde and Mason 1999). Toon *et al.* (2007, 2017) found both eastern and western mtDNA haplotypes in *eylandtensis* and eastern nuclear DNA among western samples. This population is thus of mixed phenotype and genotype and exhibits evidence of three-way intergradation. We prefer to restrict *eylandtensis* to the smaller Groote Eylandt population, as originally described. We suggest that its melanism and low-placed back band provide evidence of past contact with *papuana* across the Sahul Shelf (Toon *et al.* 2017), and that its resemblance to northern mainland magpies reflects its likely more prolonged contact with those populations.

The Tasmanian subspecies ***hypoleuca*** is of strictly defined distribution and is consistently smaller and both relatively and absolutely smaller-billed.

The New Guinean subspecies ***papuana*** is also of restricted distribution and allopatric. It is a small but large-billed magpie with melanism evident in adult females and young birds and with an incompletely interpreted variation in back plumage.

## A proposed taxonomic revision

The largely terrestrial Australian Magpie *Gymnorhina tibicen* shows pronounced adaptive and non-adaptive evolutionary distinctions from the more arboreal butcherbirds (*Cracticus* and *Melloria*) despite their close phylogenetic relationship (Kearns *et al.* 2013; Cake *et al*. 2018). Magpies are distributed across much of continental Australia and associated islands as a polymorphic species, varying in body size, bill size, bill proportion and in dorsal, tibial and tail plumage. The black back of some populations takes the form of a distinct band or saddle of two kinds, one including the upper mantle, another lower on the back. A third variety involves only females and young birds. Plumage diversity across the species' continental distribution is pronounced but morphometric variation is largely clinal and evidence of co-occurring variable traits with coincident geographic partitioning is limited.

On the Australian mainland we interpret *eylandtensis* (*sensu* Schodde and Mason 1999) as representing intergradation between *longirostris* from the western mtDNA phylogroup, *terraereginae* from the eastern phylogroup, and Groote Eylandt magpies. There is evidence also that subspecies *telonocua*, which intergrades broadly with *tyrannica*, is itself intergradient between western *dorsalis* and the eastern mtDNA phylogroup. The subspecies *terraereginae* and *tibicen* differ only in average size and individuals within the two populations are not mutually diagnosable. The four remaining mainland forms are: eastern clade black-backed and white-backed; and western clade white-backed melanistic and black-backed long-billed. Contact zones remain poorly defined apart from the black-backed/white-backed study of Burton and Martin (1976), and magpies of intergradient phenotype extend across more than ten degrees of longitude, including the whole of the Northern Territory, and of South Australia except near its eastern border. Yet individuals of each of the four forms appear diagnosable in respect of their neighbours. While the distributional extent of diagnostic phenotypes in the western pair remains incompletely determined, we propose recognising four mainland and three island subspecies (Figure 8).

*G. t. tibicen* Latham is the variably-sized eastern Black-backed Magpie.

*G. t. tyrannica* Schodde and Mason is the large White-backed Magpie with a broad tail band of south-eastern Australia.

*G. t. dorsalis* AJ Campbell is the melanistic Western Magpie of south-western Australia with western mitochondrial and nuclear DNA and possible social and other distinctive traits.

*G. t. longirostris* Milligan is the Long-billed Magpie of the Pilbara with western mitochondrial DNA but with both eastern and western microsatellite alleles (Toon *et al.* 2007). Its distributional limits and diagnostic phenotype remain incompletely defined.

*G. t. hypoleuca* Gould is the small, small-billed, white-backed magpie of Tasmania and Furneaux group Bass Strait Islands; it shows minor genetic divergence from other members of the eastern mtDNA phylogroup of Australian Magpies (Chesser and ten Have 2001; Toon *et al.* 2007; McIntyre 2022).

*G. t. papuana* Bangs and Peters is a small but large-billed melanistic magpie with white tibial and variable dorsal plumage of southern New Guinea; it is the sister taxon to the western mtDNA clade (Toon *et al.* 2017).

*G. t. eylandtensis* HL White is the smallest magpie, also melanistic and relatively long-billed, with a variable low-placed back band and narrow tail band, confined to Groote Eylandt, Northern Territory. We predict that this taxon will be shown to be a member of or closely related to the western mtDNA clade. There is some uncertainty about its diagnostic traits because of limited and/or imperfect specimen material and further analysis is called for.

## Biogeography

Pending further clarification that might arise from future genomic studies, we provide the following hypothesis. Toon *et al.* (2007) estimated that the geographic separation between western and eastern magpie clades occurred around 36,000 years ago as a result of environmental changes associated with late Pleistocene aridity. They inferred that the Tasmanian population became isolated around 16,000 years ago as sea levels rose following the last glacial maximum. Toon *et al.* (2017) subsequently estimated that contact between New Guinean and Australian magpies was lost at around the same time, as rising seas covered the Sahul Shelf; contact between Groote Eylandt and mainland magpies might have been lost soon after. Toon *et al.* (2007) identified population expansion in the eastern clade a little earlier, around 18,000 years ago.

It is probable therefore, that for some time after division into western and eastern populations, there was a period during which north-western Australian and New Guinean magpies existed in geographical continuity, as did those in south-eastern Australia and Tasmania (Toon *et al.* 2007, 2017). Expansion of the eastern isolate towards the end of that period most likely involved spread of northerly black-backed forms into northern Queensland and later across northern Australia, allowing secondary contact with western populations (Toon *et al.* 2007, 2017). This is evident in the mixed clade population of *eylandtensis* of Schodde and Mason (1999) and the eastern nuclear microsatellite signature in both *eylandtensis* and *longirostris* (Toon *et al.* 2007). However, during much of the period when western magpies occupied the Sahul Shelf, the range of the eastern clade may have been confined to south-eastern Australia, its expansion taking place towards the end of that period. Spread to the Cape York Peninsula might have occurred relatively late in the phase of eastern clade expansion.

The Eyrean Barrier is thought to have operated during several arid periods of the Plio-Pleistocene at around the longitude of present-day Spencer Gulf, Lake Torrens and Lake Eyre (Schodde and Mason 1999; Dolman and Joseph 2015). As a consequence, Eyre Peninsula has many western representatives of sister taxa separated across the barrier. There are exceptions involving the presence of eastern

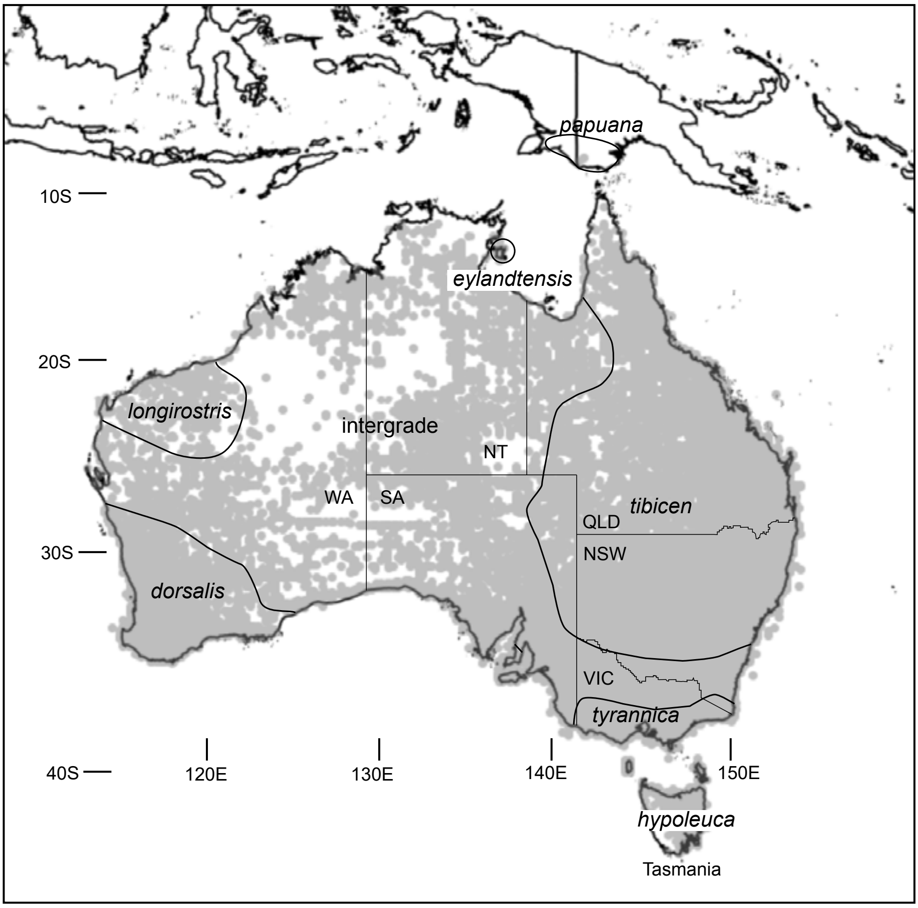

**Figure 8.** Distribution of the Australian Magpie, showing proposed taxonomic revision recognising four mainland subspecies, with approximate subspecies boundaries, and three island subspecies. State boundaries are shown with acronyms as provided in the Gazetteer.

taxa on southern Eyre Peninsula, such as Superb Fairywren *Malurus cyaneus*, Scarlet Robin *Petroica boodang*, Yellow-tailed Black Cockatoo *Zanda funerea* and White-bellied Whipbird *Psophodes leucogaster*. These birds are thought to have crossed the barrier during the period preceding the last glacial maximum when the southern Continental Shelf was exposed and covered by woodland vegetation (Dolman and Joseph 2015). The magpie might have been another to have crossed the barrier at that time. The incompletely determined genetic status of Eyre Peninsula magpies, subspecies *telonocua* of Schodde and Mason (1999) (Toon *et al.* 2007; Chesser and ten Have 2001) leaves this question open, including whether western mtDNA is residual or the result of intergradation between *dorsalis* and *telonocua*.

We have no evidence of separation of northern and southern mainland forms before the inferred division into eastern and western clades c. 36,000 years ago but later, as aridity continued to intensify, two distinctive forms have been present in both east and west. Whether such differentiation took place in allopatry is not established but appears probable in the west in view of the several phenotypic and genetic traits that distinguish that pair.

Despite the Australian Magpie's presence across much of northern Australia and even southern New Guinea, we find it likely that its origin was southern and that it underwent a typical division into western and eastern vicariants across the Eyrean Barrier. Climatic amelioration since the last glacial maximum c. 20,000 years ago has provided conditions for the magpie's population expansion and present pan-continental distribution, bringing western and eastern clades into extensive reproductive contact and blurring the distinction between populations separated earlier.

### Limitations to this study

We have reviewed infraspecific diversity in the Australian Magpie through an informal meta-analysis of published and unpublished phenotypic and genetic information. We find that neither the geographic extent of named Australian mainland subspecies nor the nature of interactions between them have been analysed to the standard recommended by many leading authors. Patten and Unitt (2002) and Remsen (2005) proposed a 95% rule when comparing a single trait between two populations, such that fewer than 5% of individuals of one group should have values overlapping 99.9% of the other and vice versa (Patten and Remsen 2017). In the case of subspecies *tibicen* and *tyrannica* such a test should be relatively straightforward but for *dorsalis* and *longirostris* the careful delineation of subspecies boundaries would be a necessary first step.

Future research showing genetic, phenotypic, social, behavioural or ecological traits coincident at geographical boundaries may further support the recognition of *dorsalis*, *longirostris* and *tyrannica* as subspecies. Further analysis of phenotypic variation is desirable among New Guinean *papuana* and Groote Eylandt *eylandtensis*. Finally, much of our current genetic insight is derived from mtDNA, with its potential to mislead in relation to hybridisation and introgression, particularly when defining species limits (Joseph 2021) but at times also within the species (Morales *et al.* 2017). Increased genetic sampling, preferably on the basis of whole-genomic data, will be important therefore in providing additional corroboration of divergence dates and events, in clarifying the nature of mito-nuclear discordance in north-western populations (Toon *et al.* 2007) and in addressing the unresolved origin and genetic basis of black-backed and white-backed plumages in the Australian Magpie.

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**Gazetteer** of Australian localities named in the text. Latitudes and longitudes are approximate.

| Locality | Latitude | Longitude |
|---|---|---|
| Adelaide SA | 34° 56′ S | 138° 36′ E |
| Arnhem Land NT | 12° 45′ S | 134° 30′ E |
| Beechborough WA | 33° 37′ S | 115° 25′ E |
| Bridgetown WA | 33° 58′ S | 116° 08′ E |
| Cape York Peninsula QLD | 12° 30′ S | 142° 30′ E |
| Carpentaria, Gulf of | 16° 00′ S | 138° 00′ E |
| Central Australia NT | c. 20° S to 26° S | 129° E to 138° E |
| Cungena SA | 32° 35′ S | 134° 43′ E |
| Esperance WA | 33° 51′ S | 121° 54′ E |
| Etadunna SA | 28° 30′ S | 139° 30′ E |
| Eyre Peninsula SA | 33° 30′ S | 135° 45′ E |
| Furneaux Islands | 40° 00′ S | 148° 00′ E |
| Gascoyne District WA | 25° 00′ S | 116° 00′ E |
| Gibson Desert WA | 23° 00′ S | 125° 00′ E |
| Great Victoria Desert WA and SA | 29° 00′ S | c. 124° E to 134° E |
| Groote Eylandt NT | 14° 00′ S | 136° 30′ E |
| Kimberley WA | 16° 00′ S | 126° 00′ E |
| Lake Carnegie WA | 26° 10′ S | 122° 30′ E |
| Lake Eyre SA | 28° 20′ S | 137° 20′ E |
| Lake Torrens SA | 31° 00′ S | 137° 50′ E |
| Langhorne Creek SA | 35° 17′ S | 139° 02′ E |
| Little Sandy Desert WA | 25° 30′ S | 121° 45′ E |
| McArthur River NT | 17° 00′ S | 136° 00′ E |
| Mount Bartle Frere QLD | 17° 23′ S | 145° 49′ E |
| Murchison District WA | 27° 00′ S | 116° 00′ E |
| Murnpeowie SA | 30° 30′ S | 139° 30′ E |
| Nullarbor Plain WA and SA | 30° 00′ S | c. 125° E to 132° E |
| Pilbara WA | 21° 00′ S | 119° 00′ E |
| Spencer Gulf SA | 34° 00′ S | 137° 00′ E |
| Yorke Peninsula SA | 34° 30′ S | 137° 40′ E |
| Yuendumu NT | 22° 15′ S | 131° 47′ E |
| | | |
| **State borders** | | |
| New South Wales NSW | From 29° S to 34–37.5° S | East of 141° E |
| Northern Territory NT | North of 26° S | 129° E to 138° E |
| Queensland QLD | North of 29° S | East of 138° E |
| South Australia SA | South of 26° S | From 129° E to 141° E |
| Tasmania | Island south of c. 41° S | From c. 145° E to 148° E |
| Victoria VIC | South of 34–37.5° S | East of 141° E |
| Western Australia WA | | All of Australia west of 129° E |