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The generic taxonomy of the Australian Magpie and Australo-Papuan butcherbirds is not all black-and-white

by Martin Cake, Andrew Black & Leo Joseph

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Summary.—Recent phylogenetic analyses showing that Australian Magpie and Black Butcherbird are sister taxa and together comprise the sister group of other Australo-Papuan butcherbirds have justified an expanded *Cracticus*. This treatment reflects earlier arguments that Australian Magpie's distinctive traits are simply adaptations to terrestrialism and not a sound basis for recognition of a monotypic *Gymnorhina*. Acknowledging the expediency of a broad *Cracticus*, we reviewed data from anatomy, plumage, nidification and voice to reassess the optimal number of genera for the group, in particular whether *Melloria* is warranted for Black Butcherbird. Australian Magpie has multiple unique traits, including many without obvious adaptive significance for terrestrial foraging or open habitat. It shares with Black Butcherbird glossy black plumage, long tarsus and deep temporal fossa, and short currawong-like calls. Black Butcherbird's rounded wing is possibly adaptive for closed-forest habitats. We recommend use of *Gymnorhina*, *Melloria* and *Cracticus* to represent this evolutionary diversity within the butcherbird-magpie clade.

The Australo-Papuan butcherbirds and Australian Magpie are usually grouped at family or subfamily rank, Cracticidae or Cracticinae, within a broader assemblage of birds including the woodswallows *Artamus* spp., currawongs *Strepera* spp., and enigmatic New Guinean peltops *Peltops* spp. Notwithstanding some views to the contrary (e.g., Johnstone & Storr 2004), most recent taxonomic reviews and global checklists (e.g. Schodde & Mason 1999, Higgins *et al*. 2006, Dickinson & Christidis 2014, Gill & Donsker 2016, del Hoyo & Collar 2016) show a trend to assigning them to two or three genera: *Cracticus* Vieillot, 1816, for the butcherbirds, monotypic *Gymnorhina* G. R. Gray, 1840, for the Australian Magpie as *G. tibicen* (Latham, 1802), and in some recent checklists (Dickinson & Christidis 2014, Gill & Donsker 2016) monotypic *Melloria* Mathews, 1912, for Black Butcherbird as *M. quoyi* (Lesson & Garnot, 1827). Australian Magpie's close relationship to butcherbirds has long been recognised (Storr 1952, Amadon 1953, Schodde & Mason 1999, Johnstone & Storr 2004). Molecular phylogenetic analysis of the group (Kearns *et al*. 2013) renewed debate over the number of genera that should be recognised. Our broad aim here is to address that question.

Three key results of Kearns *et al*. (2013) frame our review: (1) Australian Magpie is phylogenetically nested within the clade of butcherbirds; (2) within that clade its closest relative (sister species) is Black Butcherbird [*C.*] *quoyi*, and (3) the Australian Magpie / Black Butcherbird pair itself comprises the sister group of all other butcherbirds. Together, these results render *Cracticus* paraphyletic if *Gymnorhina* is retained for Australian Magpie. The most pragmatic taxonomic response to this phylogenetic result, and that advocated by Kearns *et al*. (2013), is to recognise *Cracticus* for the entire clade. That treatment had been adopted previously by some (Storr & Johnstone 1979, Johnstone 2001, Johnstone & Storr 2004, Christidis & Boles 2008, Russell & Rowley 2009) and has since been followed by others (Nguyen *et al*. 2013, Beehler & Pratt 2016). Alternatively, if *Gymnorhina* is retained for Australian Magpie then the paraphyly of *Cracticus* can be addressed either by

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assigning Black Butcherbird to *Melloria*, or placing it with Australian Magpie in *Gymnorhina*. Accordingly, our specific aim here is to assess all of the available data (morphological, molecular, behavioural) to determine which of these options is best applied.

Debate over generic assignment of the Australian Magpie has hinged on how best to interpret its traits associated with terrestriality in genus-level systematics. In choosing to advocate a broad *Cracticus*, Kearns *et al*. (2013) stressed a view that had been argued earlier: that distinctive traits of Australian Magpie solely comprise an adaptive suite and that *Cracticus* should be used for the whole group including Australian Magpie (e.g. Storr 1952, 1977, Johnstone & Storr 2004, Christidis & Boles 2008, Russell & Rowley 2009, Kearns *et al*. 2013, Nguyen *et al*. 2013, Beehler & Pratt 2016). Alternatively, it has been argued that when coupled with the bird's complex communal social system, these traits are indicative of a degree of evolutionary distinctiveness that warrants recognition at genus level (Schodde & Mason 1999, Horton *et al*. 2013).

Given agreement that Australian Magpie is indeed a terrestrially-adapted butcherbird (Kearns *et al*. 2013), the pertinent questions become whether all of its distinctive traits can be consistently interpreted in this way and how many genera should be recognised among Australo-Papuan butcherbirds. This paper seeks to answer these questions by freshly appraising the diversity and evolutionary history of the group. In particular, we test assertions in the literature that the distinctive traits of Australian Magpie are predominantly adaptations for terrestrialism (Storr 1952, 1977, Christidis & Boles 2008, Russell & Rowley 2009, Nguyen *et al*. 2013, Beehler & Pratt 2016), and that Black Butcherbird is insufficiently distinctive or divergent from other *Cracticus* to warrant a separate genus (Russell & Rowley 2009, Beehler & Pratt 2016). We also take the opportunity to correct errors in osteological criteria proposed by Schodde & Mason (1999) and cited by Higgins *et al*. (2006).

Methods

We have (i) reviewed relevant literature, (ii) examined collections held at the Western Australian Museum, Perth (WAM), Australian National Wildlife Collection, Canberra (ANWC), and South Australian Museum, Adelaide (SAMA); (iii) skulls held at ANWC and Murdoch University, Perth; (iv) reviewed data from egg collections in Online Zoological Collections of Australian Museums (OZCAM) accessed via the Atlas of Living Australia (www.ala.org), and the photographic plates of eggs in Johnstone & Storr (2004). One of us (MC) measured proportional egg shape of a representative sample (n = 287 eggs from 157 clutches) using the egg modelling plug-in for ImageJ (National Institutes of Health; https://imagej.nih.gov/ij/) developed by Troscianko (2014). This generated max. width (as proportion of length) and 'pointedness', a measure of deviation from an ellipse. We reviewed available images, including exploratory analysis of bill shape and proportions from head profile images. We reviewed vocalisations available on Xeno-canto (www.xeno-canto.org), Macaulay Library (www.macaulaylibrary.org), published audio collections (Bird Observers Club of Australia 1983–99) and commercially available digital sources (Morecombe & Stewart Guide to Birds of Australia [iOS app], PDA Solutions; Pizzey and Knight Birds of Australia Digital Edition v.1.2 [iOS app], Gibbon Multimedia). For morphometric comparisons we assembled standard measurements (wing chord, tail, culmen, tarsus length) published for all relevant taxa (Amadon 1951, Rand & Gilliard 1967, Ford 1979, Black 1986, Johnstone & Storr 2004, Higgins *et al*. 2006, Kearns *et al*. 2011), supplemented by finer-grained datasets for Black Butcherbird (Mees 1964, Ford 1983) and Hooded Butcherbird *C. cassicus* (Mayr 1940, Junge 1958). Principal component analysis (PCA) was performed (SPSS Statistics, v.22, IBM) using a rotated covariance matrix on sex-adjusted z-scores.

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Results

Australian Magpie—unique traits

Key diagnostic traits are indicated in *italics*. For simplicity, species epithets are used to refer to species (i.e., *tibicen* and *quoyi* for Australian Magpie and Black Butcherbird, respectively). In the following, Australian Magpie is named as a butcherbird (i.e., the term is used in the broad sense); the term 'core *Cracticus*' indicates all butcherbirds excluding Australian Magpie and Black Butcherbird.

Structure and bare parts

i. Markedly different proportions, with *much longer wing* and *shorter tail* relative to body length (Amadon 1951, 1953). Wing:tail ratio 1.8–1.9, cf. 1.2–1.4 in other butcherbirds (as similar to *Strepera*). PCA using published wing / tail / culmen / tarsus measurements demonstrated the clear structural differentiation of Australian Magpie vs. the remaining butcherbirds, the major disjunction from all other taxa being along principal component axes correlated to wing or wing + tarsus length (Fig. 1).

ii. Shape of *wing more pointed*, with a broad base and narrower tips forming a long triangle, particularly evident in flight (Parsons 1968, Schodde & Mason 1999, Higgins *et al.* 2006); this difference is reflected in more acutely tapered wing formula (data from Higgins *et al*. 2006) with p7 longest, compared with blunter wings in other butcherbirds, especially *quoyi* (Fig. 2). Shape of individual outer primaries also more pointed (Parsons 1968). Wing formulae for New Guinea species not available, but wing shape of *Cracticus cassicus* matches the core *Cracticus* in available flight images (e.g. Coates 1990: 376).

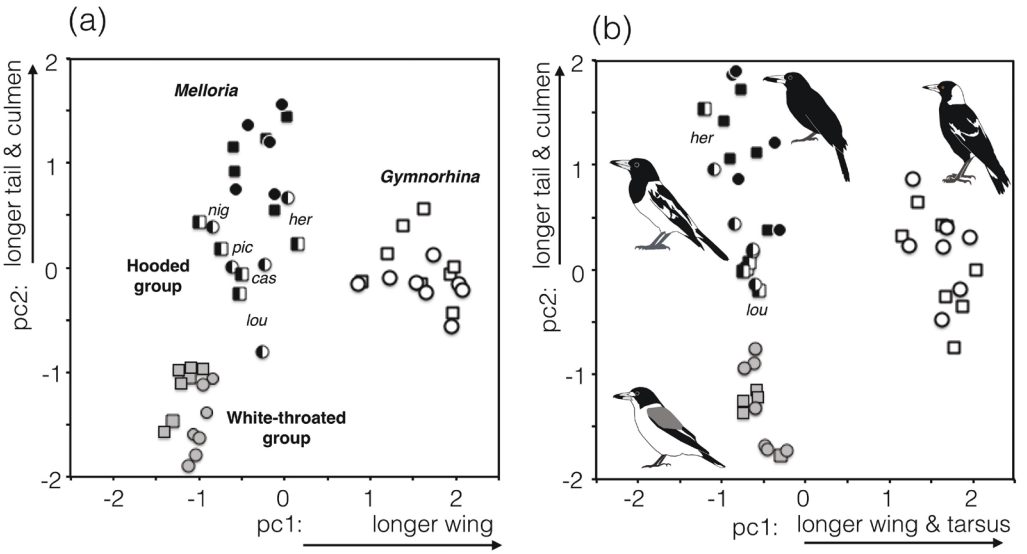


Figure 1. Principal component analysis (PCA) on sex-adjusted *z*-scores from published morphometrics of butcherbird and Australian Magpie taxa, using (a) wing / tail / culmen length, or (b) wing / tail / culmen / tarsus length. In each PCA the first two components explained >91% of the variance. In the first PCA (wing / tail / culmen), PC1 was most strongly correlated to wing and PC2 was most strongly correlated to tail and culmen length; in the second (wing / tail / culmen / tarsus), PC1 was most strongly correlated to wing and tarsus, and PC2 was most strongly correlated to tail and culmen length. Squares = males; circles = females; white = *Gymnorhina*, black = *Melloria*, grey = white-throated group, black / white = 'hooded' group taxa as labelled: nig, *Cracticus n. nigrogularis*, pic, *C. n. picatus*, her, *C. cassicus hercules*, lou, *C. louisiadensis*.

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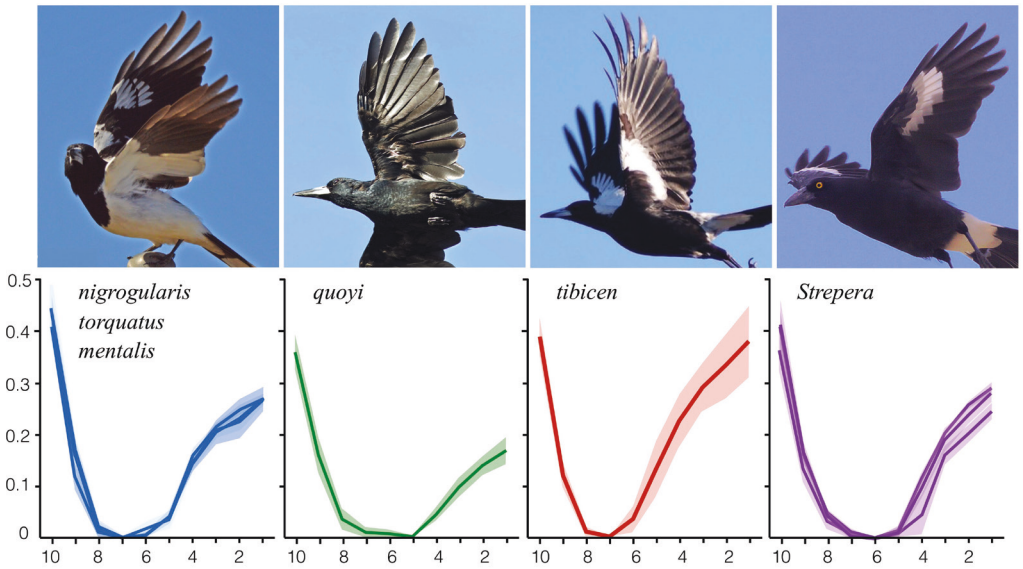


Figure 2. Wing shape and wing formula data (i.e., primary length difference from longest primary) from Higgins *et al.* (2006), scaled as proportion of total wing-chord length. Lines are centre of published range (shaded).

iii. Longer wing contains *11 secondaries*, cf. ten in other butcherbirds (Parsons 1968, Higgins *et al*. 2006).

iv. Long-legged with *long tarsus*, both proportionately (e.g. relative to body length) and absolutely (tarsus >45 mm), being closest to *quoyi* (see below). Feet and claws rather powerful, almost raptorial in character (Kaplan 2004, Higgins *et al*. 2006).

v. Semi-booted laminiplantar tarsus, vs. weakly scutellate in at least other Australian butcherbirds (Schodde & Mason 1999, Higgins *et al*. 2006).

vi. *Bill lacks prominent hook*, cf. in all other butcherbirds, tip characteristically decurved to form a sharp hook with adjacent notch in upper tomium (Higgins *et al*. 2006). Long wedge-shaped bill distinctive for the following combination of characters, although none diagnostic alone (Fig. 3): bill proportionately long and deep-based (as in *quoyi*, *Cracticus cassicus* and Tagula Butcherbird *C. louisiadensis*), with straight edge to upper and lower profile (in this closest to *nigrogularis*), and is the most steeply tapered bill of all of the butcherbirds (i.e. proportionately narrowest at bill midpoint relative to base, and forming greatest angle between culmen and mandible).

vii. *Iris brighter*, orange-brown to red-brown to red in adults, cf. dark brown in all other butcherbirds (Robinson 1956, Johnstone & Storr 2004, Higgins *et al*. 2006) vs. notably, yellow in *Strepera* and red in *Peltops*, and also reportedly paler brown in juvenile *quoyi* (Coates 1990, Pratt & Beehler 2014).

Plumage and moult

viii. Plumage *sexually dimorphic*, with mottled (or scaled) grey replacing male's brilliant white upperparts in females of all subspecies and intergrades, including on the hindneck and rump of those with black dorsal bands, and more distinctly dimorphic (black-scaled female dorsum) in white-backed subspecies *G. tibicen dorsalis*; cf. sexes

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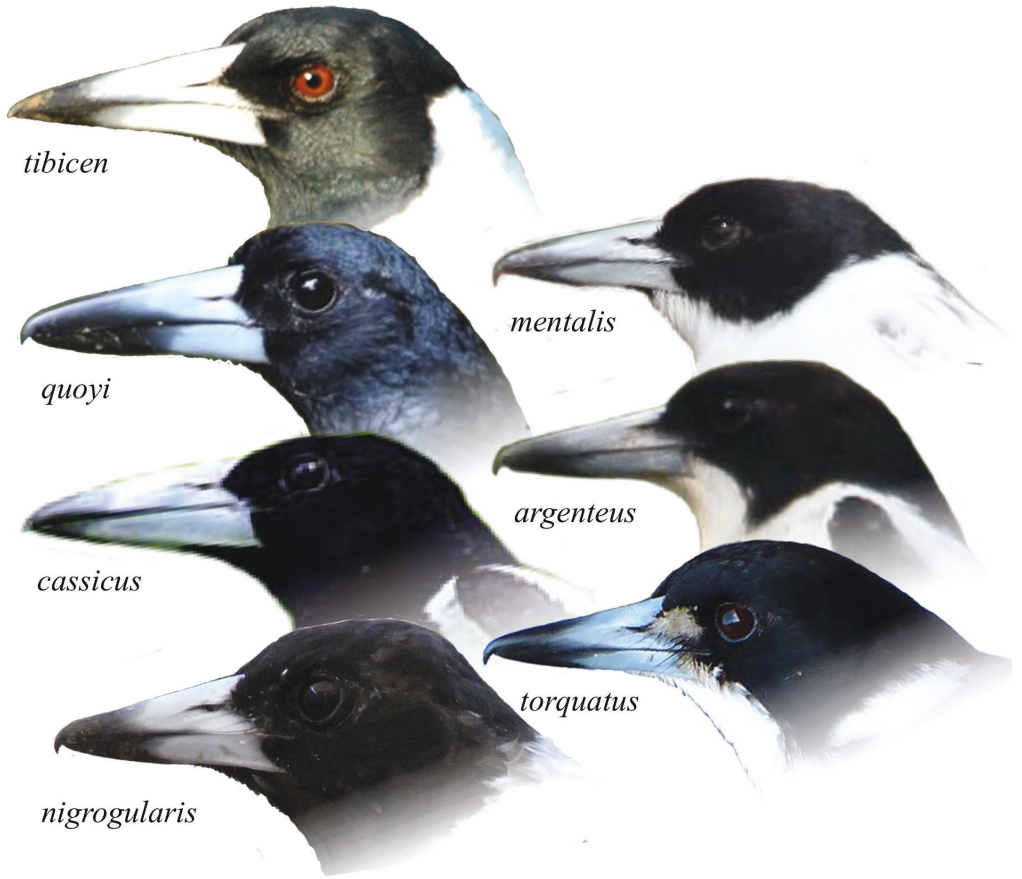


Figure 3. Typical bill and head shapes of the 'butcherbirds', proportionately scaled to mean culmen length for each taxon. Note the red eye of Australian Magpie *tibicen*, the proportionately small rounded head and glossy plumage of it and Black Butcherbird *quoyi*, and the greater extent of black on the bill of adult *quoyi*.

very similar (at most, e.g., slightly duller hood) in all other butcherbirds (Amadon 1951, Beehler *et al*. 1986, Higgins *et al*. 2006).

ix. *Slower to mature* to adult plumage, with second immature males resembling females, and males taking up to four years to reach adult plumage (Robinson 1956, Johnstone & Storr 2004, Higgins *et al*. 2006) followed by progressive whitening of rectrix shafts and narrowing of terminal tail-band for up to ten years (Robinson 1956, Black & Ford 1982); cf. one year to mature in other butcherbirds, albeit slower in Grey Butcherbird *Cracticus torquatus* which has a subtle second immature plumage (Schodde & Mason 1999). Similarly, Australian Magpie is slower to achieve adult bill colour than other butcherbirds (Robinson 1956, Higgins *et al*. 2006, Russell & Rowley 2009).

Eggs

x. Proportional *egg shape averages longer and more pointed* (this study; $P<0.0001$ and $P<0.01$, respectively) compared to all other Australian butcherbirds (Fig. 4), and presumably also *Cracticus cassicus* from published egg dimensions.

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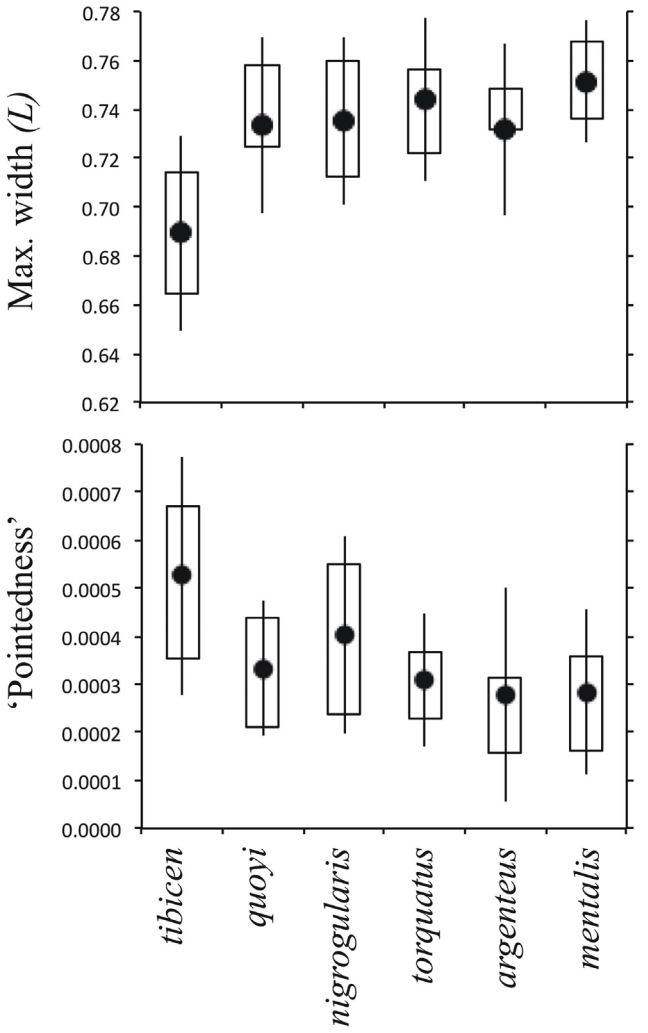


Figure 4. Egg proportions from image analysis, scaled to egg length, top: max. width (L), below: 'pointedness' (calculated deviation from ellipse shape). Box plots indicate mean (dots), upper and lower quartile ranges (box), and standard deviation (bars).

xi. Eggs *highly variable* in ground colour and character and colour of markings (Fig. 5), even at same locality, as particularly noted by Campbell (1900). Base colour most commonly pale bluish or blue-green, being closest to *quoyi* (typically pale greyish green), cf. more typically olive, brown, buff or pink tones in other butcherbirds (Campbell 1900, Beruldsen 1980, Higgins *et al*. 2006, Russell & Rowley 2009), as in *Strepera*.

xii. Egg markings include linear *streaking, scrawls and fine lines*, cf. in all other butcherbirds limited to dots, spots and blotches (Coates 1990, Higgins *et al*. 2006, Horton *et al*. 2013), as in *Peltops*, *Artamus* and most *Strepera* (although those of Pied Currawong *S. graculina* occasionally exhibit fine streaks). Egg markings less commonly concentrated at larger end, *c*.1/4 of clutches vs. 3/4 of clutches in other butcherbird species.

Behaviour

xiii. *Highly social*, with permanent group territories and complex social interactions including dominance hierarchies, across sometimes *large groups*, and forming seasonal

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Figure 5. Comparison of clutches of eggs of three species of butcherbird (Grey Currawong *Strepera versicolor*, Pied Currawong *S. graculina*, Black Butcherbird *Melloria quoyi*) and Australian Magpie *Gymnorhina tibicen* (Leo Joseph). Registration numbers in the form ANWC E20666, for example, pertain to the Australian National Wildlife Collection, CSIRO, Canberra, where the specimens are housed. Butcherbird egg plates also available in Beruldson (1980) and Johnstone & Storr (2004).

flocks of territorially excluded birds in some subspecies (Brown & Veltman 1987, Higgins *et al*. 2006); cf. other butcherbirds generally in simple pairs or, at most (e.g., in *Cracticus nigrogularis* and *C. cassicus*), small social groups mostly including previous offspring (Peckover & Filewood 1976, Russell & Rowley 2009).

xiv. *Extreme territoriality* reflected in many specialised territorial behaviours (Brown & Veltman 1987).

xv. Highly complex and *varied vocalisations*, many with complex social functions (Higgins *et al*. 2006), notably unique *carolling* behaviour as group display of territoriality (cf. simpler antiphonal duetting in other butcherbirds) and a greater range of *short calls* (see below).

xvi. *Easy walking and running gait*, rather than hopping on the ground as in other butcherbirds which are lighter and shorter-legged (Kaplan 2004).

xvii. *Feeds almost exclusively on ground*, cf. midstorey to ground-level foraging, including classic 'perch-and-pounce' hunting in other butcherbirds (Kaplan 2004, Higgins *et al*. 2006). Specialised foraging behaviour, including acoustic detection of underground invertebrates (Brown & Veltman 1987, Kaplan 2004).

xviii. Nest site usually higher in exposed crown or upper canopy of a tall tree, and occasionally nests on artificial structures; cf. typical nest sites of other butcherbirds lower in smaller trees (Beruldsen 1980, Higgins *et al*. 2006, Russell & Rowley 2009), although Pied Butcherbird *Cracticus nigrogularis* nests can be similarly exposed (Johnstone & Storr 2004).

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xix. Does not wedge or hang 'butcher' prey, as in the classic shrike-like behaviour observed in other butcherbirds; rather, oversize prey held with feet while dismembering it (Debus 1996, Higgins *et al*. 2006).

Black Butcherbird and Australian Magpie—shared traits

i. Generally *large size* (e.g. total length).

ii. Long-legged; *tarsus long*, *robust* (*pace* Mathews 1912) and *laterally flattened* (Higgins *et al*. 2006). Tarsus in smallest Black Butcherbird subspecies *rufescens* >37 mm, thus >12% longer than hooded butcherbird group, including *cassicus* of similar body weight. In considering tarsal form, it may be significant that *quoyi* forages more frequently on the ground than other more arboreal 'perch-and-pounce' butcherbirds (Diamond 1972, Peckover & Filewood 1976, Debus 1996, Beehler & Pratt 2016), and that Nguyen *et al*. (2013) noted the lateral shaft of the tarsometatarsus as shallowly concave in these species, but not other Australasian butcherbirds.

iii. Proportionately *small, rounded head*, compared to larger- and square-headed appearance of other butcherbirds (Amadon 1951, Pizzey 1980, Beehler *et al*. 1986, Coates 1990).

iv. *Bluish-green gloss* to black plumage, distinctly so in *quoyi* but slightly less so in *tibicen* in good light (Fig. 3), as also in *Peltops*; cf. in core *Cracticus*, at most a slight black gloss in good light on underparts of *nigrogularis* (Coates 1990, Johnstone & Storr 2004, Higgins *et al*. 2006).

v. Both *lack white tail tips*, a motif otherwise conserved across all other butcherbirds including *C. louisiadensis* and similarly melanistic *Strepera* species (Debus 1996); both also have *all-black remiges*, thus lacking conserved motif of white or white-edged inner 2–3 secondaries (+/- outer tertials) forming long wingbar in all other butcherbirds.

vi. In this study, skulls of both *tibicen* ($n = 7$) and *quoyi* ($n = 2$; one Australian and one New Guinean) found to have more defined and *deeply depressed temporal fossae*, resulting in relatively more prominent and thus *longer post-orbital process* due to caudal excavation (*contra* errata in Schodde & Mason 1999, repeated in Higgins *et al*. 2006); cf. temporal fossa weakly defined and shallower, with reduced caudal excavation of post-orbital process, in *Cracticus nigrogularis* ($n = 2$) and *C. torquatus* ($n = 3$). Zygomatic process and its medial accessory process typically broader based and 'bluntly bifid', although in this study these features found to be more variable within than between taxa, thus not diagnostic (*contra* Schodde & Mason 1999).

vii. Habitual use of *short calls* in vocal repertoire, including short caws, yodels and ringing notes used for social contact; vs. in other butcherbirds, short calls infrequent (cf. complex piping or rollicking song) and limited to sharp alarm notes and begging calls, plus soft croaks in *Cracticus cassicus*. Notably, Black Butcherbird calls in Queensland, Northern Territory and on Daru Island include a *kurr-ra-rung* call very similar to *Strepera graculina* (Rix 1970, Coates 1990, Debus 1996, Higgins *et al*. 2006), while certain calls of Australian Magpie, plus Black Butcherbird in New Guinea (Diamond 1972) and reportedly also the Kimberley region of Western Australia (Johnstone & Storr 2004), have a ringing quality similar to Grey Currawong *Strepera versicolor* (Fig. 6).

Black Butcherbird—unique traits

i. *Wholly black* adult plumage.

ii. Shape of *wing more rounded*, with a bluntly rounded tip in flight and less tapered wing formula (Higgins *et al*. 2006), and blunter shape to primary remiges; clearly

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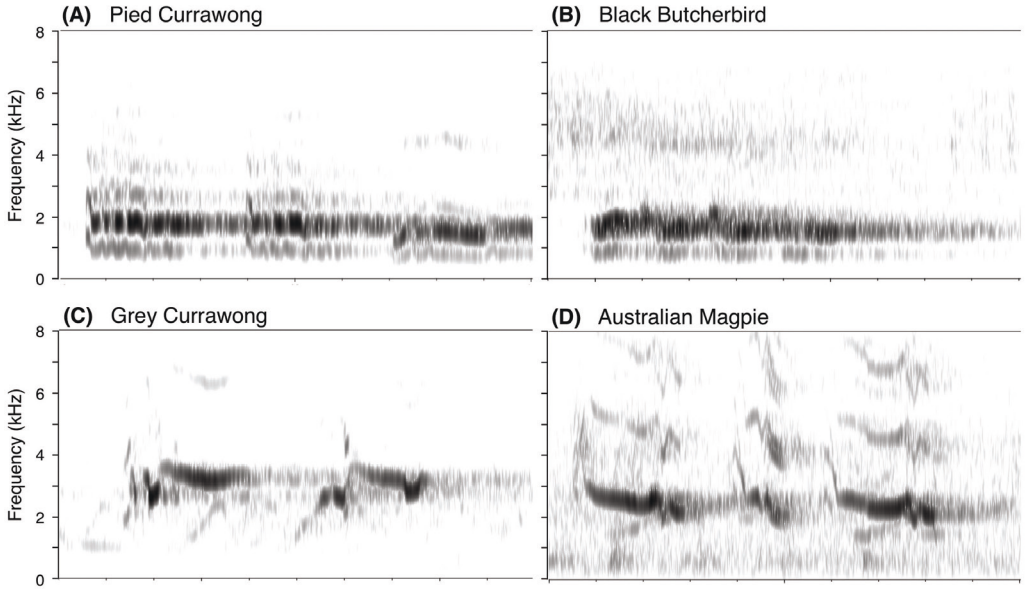


Figure 6. Representative sonograms showing similarity between the calls of *Strepera* species and some short calls of Black Butcherbird *Melloria quoyi* and Australian Magpie *Gymnorhina tibicen*. Typical *curra-wong* call of Pied Currawong *Strepera graculina* (A: near Warrumbungle, New South Wales; Marc Anderson, www.xeno-canto.org/233835) similar to *kurr-ra-rung* call of Black Butcherbird race *rufescens* (B: near Daintree, Queensland; Marc Anderson, www.xeno-canto.org/352582); *chling-chling* call of Grey Currawong *Strepera versicolor* (C: Gluepot, South Australia; Marc Anderson, www.xeno-canto.org/334453) similar to ringing flight call ('rally call') of Australian Magpie (D: Mutawintji, New South Wales; Marc Anderson, www.xeno-canto.org/335533). Each panel one second in duration.

contrasting with pointed wing of sister *tibicen*, but also divergent from other (Australian) butcherbirds (Fig. 2).

iii. Larger black tip to bill, typically half of bill length or greater, cf. distal third or less in other butcherbirds (Johnstone & Storr 2004, Higgins *et al*. 2006).

iv. Preference for denser vegetation and shaded forest interior (Diamond 1972, Higgins *et al*. 2006, Russell & Rowley 2009); where sympatric in New Guinea forest, *cassicus* is more associated with forest edge and clearings, riverine vegetation and crowns of tall trees (Rand & Gilliard 1967, Coates 1990, Pratt & Beehler 2014).

v. Behaviour more secretive and difficult to observe (Rand & Gilliard 1967, Diamond 1972, Coates 1990, Debus 1996, Higgins *et al*. 2006, Pratt & Beehler 2014).

Discussion

Genera: to split or not to split.—Given the phylogeny for the butcherbird group (Kearns *et al*. 2013), three options preserving monophyly of genera are available for its classification: (1) all species placed in *Cracticus* (i.e. recognising Australian Magpie as *Cracticus tibicen*), (2) recognition of *Gymnorhina* for Australian Magpie and Black Butcherbird, or (3) recognition of two monotypic genera, *Gymnorhina* for Australian Magpie and *Melloria* for Black Butcherbird.

While all of these options are nomenclaturally valid, we note that avian systematics in recent years has seen many genera dismantled essentially for one of three reasons (Provost *et al*. 2018). First are cases in which the relevant species are now confidently understood not to be each other's closest relatives. Dismantling *Lichenostomus* and *Monarcha* in the

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Australo-Papuan honeyeaters and monarch flycatchers, respectively (see Nyári & Joseph 2011, Andersen *et al*. 2015, Marki *et al*. 2017), or *Myrmeciza* for some Neotropical antbirds (Isler *et al*. 2013) are straightforward examples. Second are genera where the member species are not each other's closest relatives but not all relevant species have been sampled. A split is needed and either is recommended or held in abeyance until taxon sampling is completed. Arguably, these two situations are the only ones where a decision to dismantle a genus can be objective. Third are cases where the relevant species are indeed each other's closest relatives, and can validly be recognised with a single genus. Inevitably, in this case some subjectivity based on a 'weight-of-evidence' criterion is involved in decisions to dismantle larger genera into component smaller ones. For example, clear phylogenetic structure revealed by DNA studies and concordant variation in other character sets (e.g. plumage, anatomy, vocalisations) is judged as amounting to a sufficient weight of evidence to recognise different genera. Examples are the break-ups of *Aratinga* and *Ara* among Neotropical parrots (Kirchman *et al*. 2012, Remsen *et al*. 2013), *Calyptorhynchus* among Australian cockatoos (Dickinson & Remsen 2013) and *Meliphaga* in Australo-Papuan honeyeaters (Joseph *et al*. 2014). The present case is clearly excluded from the first two categories but does fall within this last, more subjective category.

Next we note the utility of smaller genera as tools for efficient communication of information on both the evolutionary history and phenotypic traits of the constituent species (Vences *et al*. 2013), and as a means for clarifying rather than obscuring the true relationships and basic patterns of the broader group (Mayr 1943). Vences *et al*. (2013) proposed criteria for optimising supraspecific classifications in this context. Their criterion of *phenotypic diagnosability* states that classifications should highlight the most important and conspicuous evolutionary changes (e.g. body plan, behaviour) such as those that are readily recognised even by non-specialists (i.e. lay recognition of [Australian] 'magpie' and 'butcherbird' morphotypes), while accepting that recognition of more cryptic groups can sometimes be necessary. A further, albeit subjective, criterion suggests that minimal taxonomic change is warranted for well-known and frequently encountered taxa (Vences *et al*. 2013) which might be invoked here. However, Vences *et al*. (2013) specifically dismissed as theoretically and practically problematic the application of a *hybrid viability* criterion, which might be argued for the butcherbirds given several records of Australian Magpie × Pied Butcherbird hybridisation (Debus 1996, Donato & Potts 2004).

Vences *et al*. (2013) further proposed a secondary *adaptive zone* criterion particularly applicable to the rank of genus, encouraging classifications defined by exploitation of a particular ecological niche. This contrasts directly with the opposing argument advocated for synonymising *Gymnorhina* in *Cracticus*, i.e., that the numerous divergent traits of Australian Magpie are unworthy of generic recognition because they represent a single correlated suite of adaptations for terrestrial foraging (Storr 1952, Christidis & Boles 2008, Russell & Rowley 2009, Nguyen *et al*. 2013, Beehler & Pratt 2016). This taxonomic dismissal of niche-driven 'ecological adaptation' also contrasts with, to use the same examples cited by Kearns *et al*. (2013), the conventional multi-generic treatment of adaptive radiations such as the Malagasy vangas (Reddy *et al*. 2012) or indeed Darwin's Galápagos finches (Sato *et al*. 1999).

Regardless, we conclude here that only a subset of the many distinctive traits of Australian Magpie are justifiably and unequivocally correlated to terrestrialism (*viz*. robust legs and walking gait, short tail accommodating a more upright stance, dorsal not ventral patterning, lack of hooked bill). If extended to include adaptation to expanding open savannas during Miocene-Pliocene aridification (Kearns *et al*. 2013), this suite might arguably also include its distinctly long and pointed wings. Counter to this is the lack of

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similar structural differentiation between savanna-dwelling *Cracticus nigrogularis* and its tropical forest-associated sister group of *C. cassicus* and *C. louisiadensis*. Conversely, we note divergence in traits with no known adaptive significance for either terrestrial foraging or open savanna habitat, but which warrant research in this regard (e.g. plumage, iris colour, egg shape and colour, moult and maturation, social behaviour, vocalisation). This suggests a pattern of general divergence (or alternatively, if implausibly, ancestral traits lost in other butcherbirds), alongside more focused niche adaptation.

The implication that all 'butcherbirds' should constitute a single genus and that the phenotypic divergence of Black Butcherbird is insufficient for recognition at genus level (Russell & Rowley 2009, Beehler & Pratt 2016) is countered with contemporary examples of genus-level radiation with weak morphological divergence but clear phylogenetic structure (see above). Examples in Australia are within the Australo-Papuan robins (e.g. *Eopsaltria* / *Quoyornis*; *Microeca* and related genera; Loynes *et al*. 2009) and honeyeaters (e.g. *Meliphaga*, *Microptilotis*; Joseph *et al*. 2014). Mathews (1912: 114) originally diagnosed *Melloria* for the Black Butcherbird by its 'stouter longer bill and longer wing and tail and stouter feet'. All but the last trait neglect some overlap in measurements between the smallest subspecies *rufescens* and *Cracticus cassicus*, especially its large island form *C. c. hercules*. Here, we instead note a number of traits shared by Black Butcherbird and Australian Magpie but not by other butcherbirds, including their long robust tarsus, glossy plumage, distinctly *deeper* temporal fossa (correcting error in Schodde & Mason 1999), and habitual use of short ringing or yodelling calls. The similarity of some Black Butcherbird calls to those of *Strepera* has been noted by others (Rix 1970, Debus 1996, Johnstone & Storr 2004, Higgins *et al*. 2006), and we note here the same similarity for some calls of Australian Magpie. These shared traits can variously be interpreted as either derived from the most recent common ancestor of Australian Magpie and Black Butcherbird, thereby affirming their monophyly, or as inherited from a more distant ancestor but correspondingly lost or modified in other butcherbirds, so affirming their divergence. Additionally we note the proportionately long inner primaries of Black Butcherbird yielding a uniquely rounded wing compared to other butcherbirds (although wing formula data are absent for New Guinean species), possibly an adaptation for its preferred closed-forest habitat, vs. the long pointed wings and open savanna habitat of Australian Magpie. These shared and unique traits collectively establish a wider morphologic and phenotypic 'gap' between Black Butcherbird and other *Cracticus* (*sensu* Mayr's 1943: 139 'decided gap' or Vences *et al*.'s 2013: 224 'phenotypic diagnosability') than has previously been appreciated. While acknowledging some inevitable subjectivity in these arguments, we suggest that the evolutionary diversity this 'gap' represents warrants emphasis at the generic level. That is, recognition of *Gymnorhina* and *Melloria* serves the biologically useful purpose of communicating this diversity. Concomitantly, we posit that their shared traits do not form sufficient argument for a shared *Gymnorhina* containing both *tibicen* and *quoyi*, as that would ignore the many unique traits of Australian Magpie, whether adaptive or simply divergent, or both, as well as diagnosability criteria we have discussed.

Conclusion

Our re-appraisal of the Australo-Papuan butcherbirds and Australian Magpie shows that the deep genetic structure confirmed by Kearns *et al.* (2013), i.e. Black Butcherbird representing a separate lineage to other butcherbirds and sister to Australian Magpie, is broadly concordant with patterns and 'gaps' in phenotypic diversity within the group. This is especially so when fully compared across structure (including wing shape, osteology), plumage, behaviour (including nidification and vocalisations), and ecological niche. We conclude that this clade of closely related species has an evolutionary history and diversity

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most usefully recognised in three genera: robust, terrestrial *Gymnorhina*; robust, forest-dwelling *Melloria*; and the smaller more gracile, more structurally and ecotypically similar core *Cracticus*. These groups broadly represent divergent radiations for open terrestrial foraging, closed-forest subcanopy, and more open woodland and forest edge, respectively. However we also note examples of divergence (perhaps ancestral diversity) lacking a clear ecological basis. We specifically refute a repeated misconception in the literature that has caused the many distinctive traits of *Gymnorhina* to be dismissed as a single suite of 'foraging adaptations' (Storr 1952, Christidis & Boles 2008, Russell & Rowley 2009, Beehler & Pratt 2016). In addition, we particularly note the shared blue-green gloss, long robust tarsus, temporal form, and short currawong-like calls of the *Melloria* + *Gymnorhina* clade, and the broad rounded wing of *Melloria*. We view these as significant to systematics when combined with distinctions previously acknowledged for all-black *Melloria* and terrestrially adapted *Gymnorhina*, and all within the phylogenetic structure outlined by Kearns *et al*. (2013). While nomenclaturally valid, synonymising *Gymnorhina* with *Cracticus* including *quoyi* (*sensu* Johnstone & Storr 2004, Christidis & Boles 2008, Russell & Rowley 2009, Beehler & Pratt 2016) needlessly discards much significant information regarding the evolutionary history and adaptive diversity of the group, as summarised above. We thus commend recognition of both *Gymnorhina* and *Melloria* (*sensu* Dickinson & Christidis 2014, Gill & Donsker 2016, del Hoyo & Collar 2016) as the taxonomic treatment best reflecting current understanding of evolutionary relationships and phenotypic diversity in the Cracticini.

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