# A guide to the evolution and classification of Australian birds in 2017

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#### Abstract

This article was first published in 'The Australian Bird Guide' (CSIRO Publishing, 2017). It is reproduced here with minor updates and modifications. Scientific names of individual species are listed in an Appendix except where pertinent to points in the main text.

The recently published Australian Bird Guide (Menkhorst et al., 2017) comes at a time of tremendous and ongoing change in our understanding of bird evolution and how the classifications we adopt can best summarize that understanding.

Imagine two Australian ornithologists, one from 1935 and one from 1975, finding themselves perusing the new field guide in 2017 when this is being written. Both recognize most but not all of the birds in it. Neither recognizes the Eungella Honeyeater (but that 1962 photograph in Emu of a supposed Bridled Honeyeater now makes more sense to our 1975 friend). The Grey Grasswren, officially described in 1968 and thus unknown to our 1935 colleague, was found in 1975 in South Australia beyond where it was first discovered around the western parts of the New South Wales-Queensland border. Western Whipbirds, thought in 1935 to be heading to extinction in Western Australia, had been confirmed in eastern Australia just two years earlier in 1933.

Both our ornithologists can see how bird names have changed and find much to talk about in this book, but it's the ways in which we now understand groups of birds to be related to each other that really animates their conversation. Chats are honeyeaters. "Well, yes, I suppose that's nearly been suggested," the 1975 worker says. Owlet-nightjars next to swifts. "Surely, you modern people have been misled!" Falcons next to parrots and not with other diurnal birds of prey. "Now you're delirious!" Budgerigars close relatives of lorikeets, the Scrub-tits of whitefaces? "Madness!" Shrewder, well-informed ornithologists of any era would wryly note that hints of these relationships were often seen in behaviour, eggs, nests, anatomy, moults and plumage.

The point here is that a revolution in ornithology, especially in systematics (the scientific study of relationships and how to classify according to those relationships), began in the late 1960s and today shows little sign of stopping because of the production of new field guides, such as the 2017 *Bird Guide*. Arguably, American ornithologist Charles Sibley started it by studying bird systematics through molecules, first proteins then DNA, and especially at the higher taxonomic levels of order and family. Since the 1980s, techniques to read and analyse DNA sequences have improved such that

we can now sample DNA from most of the genome – the full complement of DNA in a cell. DNA provides new frameworks with which to understand how species are related to each other in the avian evolutionary tree of life, or phylogeny. A well-supported phylogeny helps us assess how any aspect of bird biology has changed during the various processes of evolution.

Charles Sibley placed the birds of Australia front and centre in this global, ornithological revolution, along with those of New Guinea and New Zealand (Sibley and Ahlquist, 1985). In looking at why this happened, I hope the reader of today, if not our imaginary 1935 and 1975 friends as well, will embrace three ideas. First, science constantly refines our understanding of the avian phylogenetic tree and how we use classification from the Class 'Aves', right down to the level of the species, to summarize that understanding. There are mis-steps along the way, for sure, but that is how science, and people, work. Second, the 2017 Guide and its successors should look very different from each other and from their predecessors in the species and groups they recognize. Third, research in systematics can enliven the way one observes any bird. When observing a bird, we are looking at the latest steps in ongoing and open-ended evolution. That makes things far more interesting than if our understanding of the birds and the names we use all just stood still.

#### The Big Picture

Observing a community of birds is also akin to looking at different branches of the phylogenetic tree of birds. A brief summary of our current understanding of the avian tree of life from the roots to the tips will be helpful (see details in Jarvis et al., 2014; Prum et al., 2015). At the tree's trunk, living birds divide into Palæognathæ (ratites, tinamous) and Neognathæ (all others). The palæognaths continue to surprise. The flighted tinamous of the Americas are more closely related to the extinct New Zealand moas among the flightless ratites (emus, cassowaries and so on) than some of the latter are to each other. Kiwis appear closer to the extinct elephant birds of Madagascar (Mitchell et al., 2014). A corollary is that flight must have been lost multiple times in the evolution of palæognathous birds.

The Neognathæ, in turn, branches into the Galloanseres (waterfowls and chickenlike birds) and the Neoaves (all other birds). Research in the study of whole genomes in 2015 challenged the view suggested by similar research from 2014. It is fair to say that much of this debate centres on how, in the absence of a complete fossil record, our genomic technologies can recover from DNA any kind of signal of evolutionary events that happened a very long time ago. It is also fair to remind ourselves that while it is always tempting to think of a new study of avian relationships as being the best or final word on a topic to date (and maybe it is), the next study will likely differ (and it did — see Burleigh et al. 2015!), however slightly, but, again, that is how science works. So, while it is reassuring that the composition of most of the major groups of birds seems to be settled, there is still uncertainty as to where some of them fit on the avian evolutionary tree relative to each other. For example, it is now not debated that swifts, nightjars, owlet-nightjars, frogmouths and hummingbirds form a natural evolutionary grouping. Research published at the end of 2014 suggested that that group is embedded in the Neoaves whereas Prum et al., (2015)

placed it as the closest living relative of all other Neoaves. Other differences are apparent among the two recent genomic studies but I am struck by the commonalities more than the differences. For example, Jarvis et al. (2014) recognized that most Neoaves are in what they called the Passerea, which has several main lineages, the two main ones being so-called "core" landbirds (Telluraves) and waterbirds (Aequornithia). The Telluraves branches into Australaves (passerines, parrots, falcons, South American seriemas) and Afroaves (kingfishers and relatives, owls, eagles, woodpeckers, hornbills, trogons). Prum et al. (2015) retained the composition and structure of the Telluraves, for example, especially its two enormous component groups together in the same pattern of relationships but differs from the earlier work in how the ever-mysterious South American Hoatzin is related to them. I can live with that kind of debate! Resolution of these debates will depend on how well we can analyse any signal of the deep evolutionary past of birds that is present in their genomes.

#### A closer look

Considering some neognathous birds can deepen one's appreciation of Australia's role in bird evolution. Megapodes (moundbuilders, such as the familiar Australian Brush-turkey), Plains-wanderer and Magpie Goose each have their closest living phylogenetic connections in South America, the first being most closely related to curassows and guans, the second closest to seedsnipe, and the third to the marvellously named screamers. Indeed, the Magpie Goose when so considered is a very special anseriform bird (ducks, geese, swans). It sits on its own branch in the anseriform phylogenetic tree, South America's three species of screamers being on another and then all other living anseriforms essentially making up a third and final "very bushy" branch. Next, Australia's four smallest rails, the White-browed, Spotted, Spotless and Baillon's Crakes, far from being a cohesive evolutionary group, apparently represent three different lineages (Garcia-R. et al., 2014). The White-browed appears to be most closely related to a similarly odd African bird, the Striped Crake, and the bush-hens. The Spotted is closest to a handful of similar Porzana species worldwide, whereas Spotless and Baillon's are on a different branch as their own closest relatives. This is why they have recently been assigned to a different genus, Zapornia, which is not very closely related to Porzana. It also reminds us that a "body plan" like that of small crakes may not always be a good indicator of who is most closely related to whom.

Parrots and passerines (the latter loosely termed 'perching birds'), which turn out to be each other's closest relatives in a phylogenetically surprising result, yielded still further phylogenetic surprises. In passerine evolution, the first branching point led to New Zealand wrens in one lineage and all other passerines in the other. Similarly in parrots, the first branching point led to New Zealand's kakapo, kea and kakas in one lineage and to all other parrots in the other. Our understanding of passerine evolution has advanced steadily to the point where remembering the detail of what we have learned is a formidable task. In essence, the lineage in passerines that led to all species other than New Zealand wrens subdivided into suboscines (represented on mainland Australia only by pittas), and oscines or songbirds. The deepest lineages of the oscines are in Australia and New Guinea (Australo-Papua),

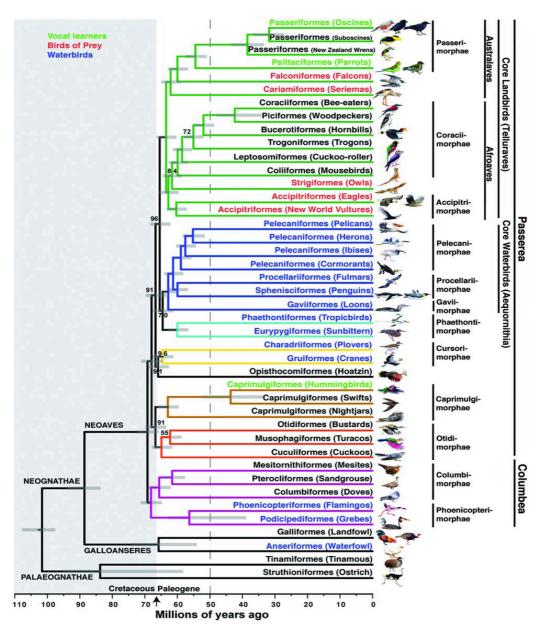


Figure 1: This figure is reproduced from a paper published in *Science* in 2014 (Jarvis et al. 2014). It is a summary or hypothesis of the relationships among the major groups of the world's birds based on an extensive dataset of avian genomes. While not the final word in pattern of relationships, the different colours used for the names of different groups indicate various aspects of avian biology and how many times they may have evolved independently. Light green names, for example, applied to oscine passerines, parrots and hummingbirds show that the biological mechanisms for learning of vocalizations have evolved independently at least twice, and red names show that predation has evolved twice.

this being our current understanding of a finding Sibley first reported in 1985 (Sibley and Ahlquist, 1985). Examples include so many birds characteristic of Australia (and New Guinea) that have no very close relatives in the Northern Hemisphere despite some having similar sounding English names: lyrebirds, scrub-birds, bowerbirds, treecreepers, whipbirds, logrunners, Australo-Papuan babblers (to distinguish them from scimitar babblers and their allies), fairy-wrens, honeyeaters, acanthizids (thornbills, gerygones and allies), whistlers, woodswallows, butcherbirds, and more. Mostly beyond Australia, an even larger group of passerine species, recently termed the Passerides, evolved and mostly in the Northern Hemisphere. One of its earliest branches, however, is the lineage of Australo-Papuan robins, and could even be largely descended from an ancestor of that group itself. Some Passerides have later ('secondarily') returned to and radiated within Australo-Papua, grassfinches being a fine example. The true thrushes, whiteeyes, swallows and martins, reed-warblers, cisticolas, and grassbirds are all in this category. Many other Passerides are only convergently similar to birds in the Australian region. Thus, treecreepers and creepers are not closely related to each other, and fairywrens are not at all close to true wrens, for example. The 1935 worker especially might need to sit down at this point.

#### Down to genus

We have seen that at higher levels of bird classification, research most often clarifies which clearly defined group is related to which other clearly defined group, rather than altering the membership of the groups themselves. What of the genus-level? Why so many perhaps unfamiliar generic names in the 2017 *Guide*? Examples will show that, in essence, much the same reasons apply.

Since 1975, several generations of ornithologists have become accustomed to some 20 species of honeyeaters making up the genus Lichenostomus. Not until 2011 did the first of several DNA studies tackle this and find that Lichenostomus in Australia was made up of at least seven different groups or lineages (Nyari and Joseph 2011; Joseph et al., 2014); the total number is eight, now that one key New Guinean species, formerly known as Oreornis chrysogenys, has finally been included in DNA studies (Marki et al., 2017). Further, at least six generic names were needed for the Australian species. Why? Five of the seven Australian groups were scattered throughout the full honeyeater phylogeny and were not each other's closest relatives, and so needed five generic names. The remaining two were indeed each other's closest relatives. They could validly be placed in a single, sixth genus or divided into a sixth and a seventh. The argument was made that because they are such distinctive lineages which diverged several million years ago, assigning them to two genera Ptilotula and Gavicalis ("plumed" and "fasciated" honeyeaters, respectively) made sense. Consider, for example, how different are the "plumed" Yellow-plumed and "fasciated" Singing Honeyeaters. The habit of using a broad Lichenostomus is dying hard, but die it must. Incidentally, the New Guinean species that was last to be included in DNA studies belongs in the genus *Micropti*lotis, itself split from Meliphaga (Joseph et al., 2014; Marki et al., 2017). And, last but not least, two species remain in Lichenostomus. One is the species on which Lichenostomus was based, the Purple-gaped Honeyeater L. cratitius, and the other is its closest relative, the Yellow-tufted Honeyeater L. melanops.

Still with honeyeaters, three species having black-and-white plumages (Pied, Black, Banded) were long placed in *Certhionyx*. They are not each other's closest relatives and must be classified in three different genera (Joseph et al., 2014).

Monarch flycatchers all look like monarch flycatchers, so they belong in the genus Monarcha. Right? No. DNA showed that Monarcha, like Lichenostomus, fell into groups or lineages of species that are not all each other's closest relatives (Andersen et al., 2015). So, again, Monarcha is restricted to the lineage that includes the single species on which Monarcha was first based, the Blackfaced Monarch M. melanopsis. Monarcha, then, is more closely related to Pacific island genera such as Chasiempis and Pomarea than to other Australian and New Guinean species formerly placed in Monarcha. So, those other species need other genera and they now fall into two genera, Symposiachrus and Carterornis. And, finally here, the Australian Magpie-lark and its close relative the Torrent-lark of New Guinea are a part of the monarch flycatcher radiation.

The importance of all this is not that names have changed — that's the least of it. It is that through systematics we grow to appreciate the spectacular evolution of even our most familiar birds. Systematics directs taxonomic changes, the details of which are governed by the rules of zoological nomenclature. All of this enhances what you see when observing a bird!

# The species level — higher hanging taxonomic fruit

Discovery of the Eungella Honeyeater, the last unquestioned species of Australian bird to be discovered *and* scientifically described (Longmore and Boles, 1983), did not mean the end of species-level taxonomy for Australian birds. Modern research documents the complex evolution still occurring at the species-population level, within and among species. We interpret this through 'lenses' of different biological characters (DNA sequences, plumage, vocalizations, and more). Interpretation through one such lens coupled with one of many ways of defining a species might suggest two populations share a gene pool and that they should be treated as one species. Another lens and another way of defining a species might suggest that they are well and truly different lineages in the avian phylogeny and that two or more species should be recognized. Reconciling these different lenses using a taxonomic system devised before Charles Darwin is akin to feeding rocket fuel to a horse pulling a cart: things may collapse! By another analogy, seeing present-day diversity through two different lenses of biological characters is akin to slicing a cake two different ways. Both have their validity but which will we follow?

Fortunately, one category of problem is simplest to resolve and again hinges on 'tree-thinking'. Until 2010, the White-naped Honeyeater Melithreptus lunatus was thought to comprise eastern Australian M. l. lunatus and south-western Australian M. l. chloropsis. DNA shows the eastern birds are more closely related to the Tasmanian endemic Black-headed Honeyeater M. affinis than to the western birds (Toon et al., 2010). We infer that the white nape-band was present in the ancestor of Melithreptus honeyeaters but has been lost in M. affinis. We could treat all three as one species (sensible? you decide!) or the western birds must be a separate, third species, M. chloropsis. In this case, the DNA evidence has in effect argued that it is time to

correct and update an earlier way of thinking based on similarities and differences.

In Golden Whistlers, Pachycephala pectoralis, separate populations in Western Australia and, mostly, South Australia characterized by cinnamon-bellied females were assigned to the subspecies Pachycephala pectoralis fuliginosa. The significance of subtle differences between them in plumage had been debated since the 1950s. DNA shows that those two isolated or at best tenuously connected populations are not each other's closest relatives. Further, the eastern (mostly South Australian) populations of "P. p. fuliginosa" are not genetically separate using the markers studied to date from other eastern Australian populations (Andersen et al. 2014; Joseph et al., 2014). Most critical of all, the western populations of "P. p. fuliginosa" are likely more closely related to another species of whistler altogether and so may not even be the closest relative of eastern Australian Golden Whistlers at all. Again, the cinnamon-belly of females in south-western and some parts of south-eastern Australia may be an ancestral character lost in some, but not all, present-day populations. Taxonomically, the south-west Western Australian populations must become a separate species, which happily does have some subtly distinct plumage characteristics, and rules of nomenclature dictate that it be known as Pachycephala occidentalis. Further study is needed to address how the re-defined P. pectoralis fuliginosa mainly of South Australia relates to other eastern Australian Golden Whistlers.

What of cases like the Crested Shrike-tit's "Eastern", "Northern" and "Western" forms where slight plumage differentiation (as we perceive it) between isolated populations has long led ornithologists to say, "They are

just subspecies"? These seem thornier, not so much because the various birds are again geographically isolated from each other, but because debate about how many species there are has never really settled on any one prevailing view. Why? I suggest this is partly because there is often an unspoken undercurrent of thinking in cases like the shrike-tits concerning how we should interpret similarities and differences. That is, to us they look so similar that the notion of them being separate species seems harder to digest despite any differences and similarities in vocalizations or behaviour. If some other differentiating character appears, such as vocalizations, coupled with whether their ranges overlap naturally or not, two species may become accepted. Think of the very similar-looking Chirruping and Chiming Wedgebills, which sound so very different and occupy different habitats where they approach each other geographically that their recognition as two species now goes unremarked. DNA evidence supports this (Toon et al., 2013). Critically needed research on isolated populations like the shrike-tits won't change the reality of their existence: birders should want to see and hear them all! As with the Melithreptus honeyeaters and whistlers, research is needed to reveal one or other of a fairly small number of predictable patterns of relationships among them. The problem then is in interpreting patterns among such isolated populations under the Biological Species Concept, ornithology's dominant definition of a species since the mid-20th century. It requires that we venture to supposition at the edge of science. Does it matter whether they could interbreed if they came together, which clearly they aren't about to do? Does the degree of differentiation between some other closely related pair

guide us? I ask, "Is this the best our science can do today?" I hope not. Alternatively, in the case of such isolated populations about which there is taxonomic debate, we are interested in how they are related to each other in the avian phylogeny, how similarities and differences in other traits can be interpreted in a framework of well-understood evolutionary relationships and, perhaps, a different species concept, whether gene flow has ceased among them, and whether they are continuing to diverge even if there is gene flow, however occasional. We can test that using data and analyses of those data that can be repeated. That is science. So, I suggest that the species or subspecies question is interesting for very different reasons these days but, nonetheless, debate about it won't go away, especially where isolated populations are concerned. I suggest that it will often be more interesting and useful to first examine how the isolated populations are related to each other. Then we can ask whether some phenomenon like gene flow, say between two and not a third, is affecting their divergence. Finally, does all of that dictate an alternative approach to classification?

An example that involves present-day isolated populations and past gene flow will help here. Debate has long been whether Grey and Silver-backed Butcherbirds are one or two species. We now know that Silver-backed Butcherbirds are the closest relatives of a third bird, the Black-backed Butcherbird. The Grey Butcherbird is, in turn, the closest relative of the other two. Recent research (Kearns et al., 2014) gave a twist: genes from Grey Butcherbirds entered into eastern populations of Silver-backed Butcherbirds, probably some 20,000 years ago, and have now spread west through Silver-backed Butcherbirds. Only in the westernmost parts of Silver-backed's range is the relevant piece of DNA still in its "pure" Silver-backed Butcherbird form, and closest to that of Black-backed Butcherbirds. Silver-backed and Grey cannot be regarded as the same species. Hybridization and gene flow has, we argue, occurred among species that are not closest relatives, that pattern of relationships having been established much earlier in butcherbird evolution. In other words, hybridization need not mean that the birds involved are closest relatives. A classification reflecting evolutionary history is not achieved by making Grey and Silverbacked the same species because of past gene flow. A very similar example concerns the Pale-headed, Northern, and Eastern Rosellas. Pale-headed and Northern Rosellas are closest relatives and can be recognized as two species. Genes from the Pale-headed appear to have extensively "infiltrated" Eastern Rosellas of the mainland but not Tasmania. Eastern Rosellas must nonetheless be regarded as a third species (Shipham et al., 2015, 2017). Recognition in the 2017 Guide of the Copper-backed Quail-thrush as a species separate from the Chestnut Quailthrush arose from an example of this kind of research into past gene flow having been explored (Dolman and Joseph, 2016).

By telling us about the phylogeny — the evolutionary history or evolutionary footprint of a species or population — we can learn something about biogeography: how species evolve as landscapes also evolve and climates change. They tell us that the Tasmanian population of Eastern Ground Parrots, for example, still share genetic diversity with mainland eastern Australian populations despite current isolation by Bass Strait. The Western Ground Parrot, however, is weakly

but consistently differentiated in plumage and shares no diversity with any eastern birds for the piece of DNA so far studied (Murphy et al., 2011). Recognizing these as two species says that until we can demonstrate genetic connections between western and eastern populations, we interpret the available data as favouring the idea ('hypothesis') that they are two lineages not exchanging genes and that we should call them two species. Further, we can suggest why they look so similar: strong natural selection for camouflage to avoid predation. Indeed, the unquestionably different species, the Night Parrot, is in many ways not so different in appearance, so its plumage, too, is probably under similar long-term evolutionary pressure. This reiterates potential traps of relying on differences in plumage. Australian populations of the Spectacled Monarch most definitely are two genetic groups with respect to mitochondrial DNA, but these in no way match geographical structure in their plumage variation. Research is still in progress to examine why this is so; the answer, I suspect, will again involve how well we can understand intricacies of the population genetics of the species in its past.

Lessons have been learned about how important it is to understand what we might call DNA's own natural history. DNA studies of two pairs of Australian birds well illustrate one potential interpretative trap. One pair of species is the White-browed and Masked Woodswallows, and the other is the Grey and Chestnut Teals. What we have learned from these two pairs concerns multiple species that have diverged from their most recent common ancestor only very recently in evolutionary terms. It may be that we can see (or hear) very clearly that they are distinct species. Some of the DNA we study, especially

mitochondrial DNA, may not have "caught up" yet, as it evolves more slowly than, say, plumage and the genes controlling plumage differences. Certainly, in the teals and perhaps in the woodswallows, those genes may well even be located on the sex chromosomes, whereas their pool of diversity for mitochondrial DNA may still essentially be that of their common ancestor (Joseph et al., 2006; Dhami et al., 2016). Alternatively, testing for a role of natural selection at the level of DNA itself can be critical. This has, we believe, led to the best approach to understanding some truly remarkable patterns of genetic diversity in the Eastern Yellow Robin. Within that species, there is a geographically structured but extraordinarily deep genetic break in mitochondrial DNA diversity between two groups of populations. The magnitude of this break is more typical of that seen between genera than within a species. We have argued, however, that it is best interpreted as evidence of selection on mitochondrial DNA, and that there is no need to alter subspecies or even species-level classifications (Morales et al., 2015, 2017).

Geographical overlap of migratory and non-migratory populations also needs disentangling by field, museum and laboratory work. The mystery of how many species should be recognized in the Cicadabird, which by our current understanding also occurs widely outside Australia, is a fine example (Pedersen et al., in press).

I hope all this gives a taste of the complexity of these species-level problems and why they will be around for a while yet. Each case will be different. Patterns of relationships and what gene flow does or does not mean with regard to whether it is stopping divergence between two populations will be critical. The 2017 *Guide* is a treasure chest of

the problems waiting for study. How many species are in the Purple Swamphen, Spinifex Pigeon, Red-tailed Black-Cockatoo, Helmeted Friarbird, Spectacled Monarch and Cicadabird, to name a few? Are the three *Polytelis* parrots (Superb, Regent and Princess) more closely related to each other than one or two of them are to other parrots? While reassuring our friends from 1935 and 1975 that we have made strides, they'd delight in reminding us of the old maxim — the more we learn, the more questions we find. And that is as it should be.

### Appendix

Scientific names of species mentioned but omitted in the text for clarity of reading

Australian Brush-turkey Alectura lathami Plains-wanderer Pedionomus torquatus Magpie Goose Anseranas semipalmata White-browed Crake Amaurornis cinerea Spotted or Australian Crake Porzana fluminea Australian Spotless Crake Zapornia tabuensis (Porzana tabuensis in some texts) Baillon's Crake Zapornia pusilla (Porzana *pusilla* in some texts) Grey Teal Anas gracilis Chestnut Teal Anas castanea Australasian Purple Swamphen Porphyrio melanotus (Porphyrio porphyrio in some texts) Hoatzin Opisthocomus hoazin Spinifex Pigeon Geophaps plumifera Budgerigar Melopsittacus undulatus Red-tailed Black-Cockatoo Calyptorhynchus banksii Superb Parrot Polytelis swainsonii Regent Parrot Polytelis anthopeplus Princess Parrot Polytelis alexandrae Pale-headed Rosella Platycercus adscitus Northern Rosella Platycercus venustus

Eastern Rosella Platycercus eximius Eastern Ground Parrot Pezoporus wallicus Western Ground Parrot Pezoporus flaviventris Night Parrot Pezoporus occidentalis Grey Grasswren Amytornis barbatus Eungella Honeyeater Bolemoreus hindwoodi Bridled Honeyeater Bolemoreus frenatus Yellow-plumed Honeyeater Ptilotula ornata Singing Honeyeater Gavicalis virescens Helmeted Friarbird Philemon buceroides Scrub-tit Acanthornis magna Copper-backed Quail-thrush Cinclosoma clarum Chestnut Quail-thrush Cinclosoma castanotum Western Whipbird recently advocated to be Psophodes nigrogularis and Psophodes leucogaster Chirruping Wedgebill Psophodes cristatus Chiming Wedgebill Psophodes occidentalis Crested Shrike-tit Falcunuclus frontatus Spectacled Monarch Symposiachrus trivirgatus Cicadabird Edoliisoma tenuirostre Grey Butcherbird Cracticus torquatus Black-backed Butcherbird Cracticus mentalis Silver-backed Butcherbird Cracticus argenteus White-browed Woodswallow Artamus superciliosus Masked Woodswallow Artamus personatus Eastern Yellow Robin *Eopsaltria australis* 

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