

Book Reviews

WHAT AFTER CHRISTIDIS AND BOLES?

**AN EXTENDED REVIEW OF
SYSTEMATICS AND TAXONOMY
OF AUSTRALIAN BIRDS BY LES
CHRISTIDIS AND WALTER E. BOLES
2008.**

CSIRO Publishing, 278 pages, \$69.95.

This book (hereafter C&B 2008) was long awaited. It succeeded the authors' earlier "The taxonomy and species of birds of Australia and its Territories" (1994) (C&B 1994) which became the accepted list of species for Birds Australia and Birds S A. Neither monograph provided a list of subspecies for official adoption. The reasons for the 14 year gap between the two books and the eager anticipation of the second were the same: much had changed but much more remained (and remains) uncertain. The authors drew conclusions where they could but when the evidence proved inconclusive they generally retained the *status quo*.

The title of the book is itself of interest. Some might think of systematics and taxonomy as synonymous, but systematics combines phylogenetics (or evolutionary descent) with taxonomy. C&B 2008 takes us through the phylogenetic evidence and argument relevant to every order and family occurring in Australia and then provides the (taxonomic) list of species in each family.

Stated simply taxonomy is a method of classifying and naming living forms to reflect their evolutionary relationships to one another, their phylogeny. Accepted taxonomic names are essential for all observational studies and for meaningful management and conservation. Taxonomy also informs us about the differences between birds or their similarities to one another and why those superficial comparisons may, or may not, reflect their phylogeny closely. Many birds that look alike may be only distantly related (convergent evolution) while others that seem very different are closely related in the evolutionary sense. Taxonomy will keep changing as long as we continue learning about evolution.

In the *Introduction* the authors stated the ground rules for their taxonomic decisions, relying where possible on well supported data and argument in peer-reviewed publications, and using unpublished material only in deciding between plausible but competing claims, though it is not always clear when they resorted to the latter

In the *Foreword* Allison Russell-French and Stephen Garnett commented that "taxonomy (had) become ever more sophisticated". Taxonomists still measure and compare skins on a bench, but increasingly incorporate behavioural, ecological, bio-geographic, anatomical and, over the last four decades, genetic evidence. Another major change has been the increasing application of cladistics (Hennig 1966) and other phylogenetic methodologies in which characters that vary among populations are analysed to produce cladograms or phylogenetic trees that

demonstrate the hypothesised branching nature of evolutionary progress. The data analysed can be of differences in morphology or any other variable and increasingly they are molecular genetic data, particularly DNA sequences. The statistical procedures and computer programs needed to interpret these data provide a repeatable and clearer picture of hypothesised branches (clades) in the evolutionary “tree of life”. In particular these methodologies are better able to distinguish similarities that are shared because of inheritance from the most recent common ancestor from those that have evolved independently, i.e. convergently, or have been retained from a more distant ancestor.

These phylogenetic techniques provide the basis for many of the ideas reshaping our views about the evolution of birds and the way we should classify them, but highlight two perennial challenges to taxonomic practice. Firstly, as the authors pointed out, nodes present at the junction of clades may be placed at any point from deeply within the phylogenetic tree to superficially, indicating either ancient or more recent separation of lineages respectively. This causes difficulty in finding an accepted way of naming natural assemblages of a rank intermediate between those within the conventional hierarchy of Class, Order, Family, Genus and Species. Although the authors discussed this challenge extensively only Orders and Families head the *Lists*. The second matter, more directly addressed by C&B 2008, is the difficulty of translating a three dimensional phylogenetic tree into a one dimensional taxonomic list. Such a linear list can be improved with judicious use of intermediate ranks such as Subfamily or even by placing a line between well supported clades within a Family. Moreover the phylogenetic tree has a fourth dimension, time: some taxonomic entities evolve more rapidly than others.

From the 1960s, protein analysis provided objectivity for the genetic basis of avian phylogeny, and more direct genetic evidence

came two decades later with the DNA-DNA hybridisation studies of Sibley and Ahlquist (1990) and their colleagues. They showed that one of two major radiations of typical passerine birds (the oscines) originated in Australo-Papua, probably after the separation of the Australian continent from Antarctica, and that most Australian passerine groups were more closely related to each other than to the Eurasian groups they resembled and with which they had been associated traditionally. They also made substantial changes in the arrangements of non-passerines. Subsequent studies, including DNA sequencing, have confirmed some of that early work and have shown moreover that Australo-Papua is the centre of origin of the whole oscine radiation (see Christidis and Norman 2010). In general molecular genetic studies can detect divergences between Orders, Families and Genera with some consistency but conflicting data continue to appear, for reasons that are beyond the scope of this review. Moreover a recent cladistic study of higher order taxonomy (Order and Family) that analysed 2,954 morphological characters (Livezey and Zusi 2007) failed to support a number of the counter-intuitive changes suggested by recently published DNA studies such as those of Fain and Houde (2004, 2006), but was published too late for C&B 2008 to consider its conflicting claims fully.

It is well to recognise some of the difficulties associated with analysing the quantity of information involved in cladistic examination of data. Generally a number of different ways of analysing data (algorithms) are run to generate and test phylogenetic hypotheses, including sophisticated statistical techniques such as “maximum likelihood”, “maximum parsimony” (no more entities than are needed, after fourteenth century William of Ockham) and “Bayesian analysis”, the last a development of the product of probabilities theorem of eighteenth century vicar Thomas Bayes. Even in rigorous studies there may be an element of uncertainty in the outcome, and C&B 2008

made the salient point that confirmation by independent researchers, using complementary methods, is highly desirable although rarely available. Significant difficulties apply, particularly to deeply placed nodes that are close to one another and, as discussed below, to recently evolved species.

It is of some interest to understand to what extent genetic data were used in deciding which Australian birds should be accorded species rank (see Maclean et al. 2005 for an introduction to this subject). When making determinations entirely from morphological characters C&B 2008 followed the practical (British) guidelines of Helbig et al. (2002). But in "assessments of published genetic data (they) attempt(ed) to provide similar treatments to taxa with comparable levels of differentiation." If by differentiation they were referring to genetic divergence this statement is difficult to accept fully because species may be separated by very variable genetic distances that are sometimes considerable, but at others barely detectable. The White-browed and Masked Woodswallows are a case in point (Joseph et al. 2006). C & B 2008 also asserted that "species (within an Order or Family) should reflect roughly equivalent distinction from one another". This assertion is unsustainable because it makes little or no allowance for taxa separated by greater or lesser genetic distances, unless other categories are applied such as subgenus, super-species, semi-species and subspecies. The last category was certainly discussed by C&B 2008 but no definition was offered because, as in their earlier publication, the species is the lowest rank included within the scope of their work.

An outline follows of notable changes made to the list since 1994. For an incisive examination the most fundamental re-arrangements of C&B 2008 and of alternative ideas for future change read Joseph (2008); for other views including the peripheral relevance of vagrants and off-shore records read Low (2008) and Scofield (2008) and for a full list of changed species names see

Debus (2008a, 2008b) and Dutson (2008).

In C&B 2008, in accordance with recently published genetic evidence, notably Fain and Houde (2004, 2006), tropicbirds do not belong with pelicans and cormorants but form a separate order and are in a different major clade (Metaves) that includes the orders of grebes, flamingoes, pigeons, nightjars (+ frogmouths) and swifts (+ owlet-nightjars). Penguins and seabirds are in another major clade (Coronaves) with pelicans which belong with the order of storks and herons, not with cormorants and darters. The taxonomically enigmatic button-quail are placed in an expanded charadriiform order as one of thirteen families represented in Australia. It is sobering that none of these changes is supported by the cladistic morphological study of Livezey and Zusi (2007) whose taxonomy would be more familiar to us. Only future studies, using complementary methods will determine to what extent and how these two very different taxonomies can be reconciled. In the passerines (also in Coronaves) the bristlebirds, scrub-wren-thornbill group and pardalotes have been restored to separate families, rather than lumped as in C&B 1994. Drongos too have been placed again in a family separate from the fantail-flycatcher group which itself is divided into two families, separated provocatively by shrikes and corvids. The cisticolas, reed-warblers and megalurids (including songlarks) are restored to three separate families. The Mistletoebird rejoins the sunbirds and the white-eyes join the largely extra-Australian timaliid babbler family. Pipits and wagtails (Motacillidae) are listed amongst several families of finches, and the old world Greenfinch and Yellowhammer come last, not starlings as in C&B 1994 or corvids as in our earliest field guides.

C&B 2008 placed the magpie *Gymnorhina* in *Cracticus* with the butcherbirds, evidently choosing to overlook its more complex social structure, adaptation to a terrestrial lifestyle, several anatomical differences as outlined

by Schodde and Mason (1999), its black-tipped white tail compared with the white-tipped black tail of both *Cracticus* (except for divergent *C. quoyi*) and *Strepera* or its more diversely decorated eggs. If these features might not justify the erection of a new genus, its abolition seemed to serve little purpose (Joseph 2008) and the authors' stated reasons for it were unconvincing. DNA studies and their interpretation would of course be pertinent to this question.

The arrangement of honeyeaters is also novel, though underpinned by a DNA-based review of this family by Driskell and Christidis (2004) that regrettably contained analytical errors now addressed in part by Gardner et al. (2010) who have shown, for example, that *Lichenostomus* consists of at least three genera. The former study showed that spinebills diverged early from all others, which are grouped within four further clades (three only in the latter study), each containing both large and small honeyeaters. Miners and wattlebirds are placed in clade one and friarbirds in clade four. The Australian chats are in clade two where they are listed between the Grey Honeyeater to which they are quite closely related, and the Black Honeyeater to which they are related only remotely. It is unclear why the four clades are listed in this order rather than with the chats last. The problem here is that, while the chats have not diverged very far genetically from their medium- to short-billed closest honeyeater relatives, so far as it has been investigated, their common ancestors must have made a relatively rapid evolutionary change in both phenotype and lifestyle. This is the kind of mismatch of morphology and genetics highlighted by Joseph (2008) and freely acknowledged by C&B 2008. Joseph (2008) points out that traditional Linnaean classification is incapable of incorporating both the differences that we can see and the molecular information that can be discovered and has called for "an altogether different approach".

There are six new species added to the continental list. Most are through simple splits, taxonomic revisions that recognise as two sibling species what were treated previously as allopatric subspecies, viz. the Kalkadoon Grasswren *Amytornis ballarae* (from Dusky Grasswren *A. purnelli*); Kimberley Honeyeater *Meliphaga fordiana* (from White-lined Honeyeater *M. albilineata*); Western Wattlebird *Anthochaera lunulata* (from Little Wattlebird *A. chrysoptera*); Arafura Fantail *Rhipidura dryas* (from Rufous Fantail *R. rufifrons*) and Buff-sided Robin *Poecilodryas cerviniventris* (from White-browed Robin *P. superciliosa*). Schodde and Mason (1999) had recognised all but the Kimberley Honeyeater of these additions as well as others that are not included in C&B 2008. The sixth new species is the Short-tailed Grasswren which, despite its superficial similarity to the Striated Grasswren *Amytornis striatus*, is quite distinct and is genetically not its closest relative (Christidis 1999). It is therefore re-established as a full species *Amytornis merrotsyi* as described by Mellor (1913) and has been shown subsequently to consist of separate Flinders Ranges and Gawler Ranges subspecies (Christidis, Horton and Norman 2008).

Compiling a list of species and determining their number depends on how a species is defined. C & B 2008 employed the traditional Biological Species Concept (BSC) where species are "groups of interbreeding natural populations that are reproductively isolated from other such groups". They argued against using the most common alternative, the Phylogenetic Species Concept (PSC), in which a species is "the smallest cluster of individual organisms that is monophyletic (has a shared ancestry and descent) and diagnosable (distinguishable) from other such clusters by a unique combination of fixed character states". Had C&B 2008 used the PSC their list would contain more species because many subspecies would be elevated to species rank.

Another matter is whether Australias' (and South Australias') avian bio-diversity is truly represented in C&B 2008. The conventional BSC employed by C&B 2008 has the capacity to address biodiversity more fully by the inclusion of subspecies, but this is a challenging and controversial task (Patten and Unitt 2002; Rising 2007). Schodde and Mason (1999) listed subspecies for Australian passerines (as ultrataxa) and thereby complement the C&B 2008 species list. The PSC accounts for many well differentiated isolated populations that are often called subspecies under the BSC. A recent New Zealand list (Holdaway, Worthy and Tennyson 2001) used the PSC, thus recognising many island forms, but there are greater uncertainties about its practicality for a continental avifauna, particularly over the issue of hybridisation between populations. In addition both concepts share the same uncertainties in defining the boundaries of any rank, including that of species, not to mention the extent to which genetic data are integrated into determinations of taxonomic status. Under the PSC the Naretha Parrot, *Northiella (haematogaster) narethae*, and Nullarbor Quail-thrush, *Cincoloma (cinnamomeum) alisteri*, would certainly be full species, as would two or three Ringnecks, *Barnardius* spp., (Joseph and Wilke 2006), potentially at least three in the particularly enigmatic Crimson Rosella, *Platycercus elegans*, complex (Joseph et al. 2008) and three or more in the Splendid Fairy-wren, *Malurus splendens*, complex (Kearns et al. 2009). One other South Australian subspecies that might warrant species status under the PSC is the Samphire Thornbill, *Acanthiza (iredalei) rosinae*. The "Ngarkat" Fieldwren, *Calamanthus (campestris) winiam*, "Ngarkat" Thornbill, *Acanthiza (iredalei) hedleyi*, the two isolated Chestnut-rumped Heathwren, *Hylacola pyrrhopygia*, subspecies *parkeri* and *pedleri* and the Kangaroo Island Whipbird, *Psophodes (leucogaster) lashmari*, are further candidates, but, since their phenotypes differ rather more subtly, unless they show pronounced genetic divergence, they are less likely to receive

recognition except as subspecies under the BSC. In the case of the Magpie (*Gymnorhina/ Cracticus*) this is likely to remain a single species under any concept. Schodde and Mason (1999) recognised eight ultrataxa (subspecies) based on morphological features but the molecular work of Hughes and colleagues (Toon et al. 2007) showed a quite different picture, a clear genetic break between eastern and western populations but no correlation with these divisions. They did not accept any taxonomic division within the species. Borderline examples will occur in the PSC as in any system and it would be difficult for any one or two persons to produce an Australian taxonomic list that would satisfy all other taxonomists completely.

An important question is how we might keep Australian bird taxonomy up to date with future research and/ or in line with other taxonomies; some changes have been foreshadowed already by Christidis and Norman (2010) and others by Gardner et al. (2010). In an early response to this question Les Christidis suggested (pers. comm.) that it could be through regular annual revisions in *Emu* but it might be preferable to form a standing committee that can maintain a current taxonomy and make collective revisions as, for example, in Britain, North America and South America. The first task will be to establish working guidelines and these need not include the long debated and never resolved argument whether to employ the BSC or PSC (see Helbig et al. 2002 and de Queiroz 2007). C&B 2008 and Joseph (2008) felt it unfortunate that these two concepts both use the same term "species". This seems surprising in relation to such a key term and concept as species. The PSC and phylogenetic methods are not synonymous as is sometimes implied. Helbig et al. (2002) accepted as a working definition of species the general lineage concept of de Queiroz (1998), "evolutionary lineages maintaining their integrity with respect to other such lineages through time and space", a clear evolutionary interpretation of the notion and one that directs the (always provisional) decisions of the Taxonomic Sub-committee of the British

Ornithologists' Union.

As readers of the *South Australian Ornithologist* will know C&B 2008 is a scholarly treatise, a major review of Australian avian systematics that has promoted immense interest and discussion. It has provided a modern Australian taxonomy but, like any taxonomy, it is a work in progress; there remain many unresolved issues that are worthy of debate among Australias' taxonomists.

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