

Introduction to the checklists of the vertebrates of Western Australia

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INTRODUCTION

This publication of the Western Australian Museum presents, for the first time, a comprehensive listing of the vertebrate animals recorded from Western Australia and the surrounding seas. The publication is primarily designed to satisfy a growing demand for an authoritative listing of Western Australian vertebrates for 'official' governmental usage. However, it is also intended to satisfy a wider audience who may require information of various kinds regarding the fauna of the state, including students at all levels, fellow taxonomists and members of the public with a special interest in our uniquely fascinating native vertebrate fauna.

The task of preparing and maintaining regional fauna checklists has long fallen to museums around the world. This reflects the concentration in museums not only of the vast bulk of the world's fauna collections, but also a sizeable proportion of its community of taxonomic specialists. The Western Australian Museum, established in 1891, is by world standards, a relatively new institution. However, its collection of almost 300,000 regionally-derived vertebrate specimens, representing more than 4600 taxa, has few equals in either size or diversity. The Western Australian Museum's history of contribution to vertebrate taxonomy is also highly distinguished, coloured by the careers of such prolific vertebrate taxonomists as Ludwig Glauert, Glen M. Storr, Gerald R. Allen and Darrell J. Kitchener. The present series of Checklists are dedicated to the labours of these former staff members, who between them laid much of the foundation of our current understanding of vertebrate diversity in Western Australia.

Why publish a checklist?

The major function of a formal checklist is to provide an authoritative reference to the scientific names of a particular group of organisms. However, a checklist is more than a simple list of names. By including a particular taxon on a checklist, the author is expressing an opinion that the particular scientific name is not only available under the terms of the International Code for Zoological Nomenclature, but also that it is the earliest available and thus correct name for a valid

biological entity – usually a species or sub-species. These decisions often follow established views and usage, but in some cases they may represent an otherwise divergent opinion based on the author's own original research or novel interpretation of previously available evidence. Where the content of these checklists departs significantly from existing compilations, we have endeavoured to provide adequate justification in the footnoted comments or by reference to appropriate sources.

Increasingly, checklists are also coming to be viewed as syntheses of biodiversity information, and are used extensively as such in both academic and management contexts. In certain circumstances, inclusion on an official list may even be prerequisite for allocation of scarce conservation funds or instigation of protective measures. In this regard, checklists are rapidly taking on a significant political role in addition to their more usual scientific one.

Other potential functions of a checklist, depending on the particular style and content, are to provide an insight into contemporary systematic thinking and to stimulate, perhaps even guide, future research. In order to enhance this latter function, we have attempted through our footnoted comments to highlight a number of species and higher taxa in such cases where available evidence supports the presence of additional taxa or the need for revision of supraspecific taxa. However, since many groups of vertebrates have not been subject to modern taxonomic study, the series of accompanying notes should not be taken as an exhaustive catalogue of unresolved taxonomic issues. In reality, there are probably many more as yet unidentified problem areas.

The future of the checklists

As indicated above, the task of cataloguing the vertebrates of Western Australia is far from complete. Among the various groups of fishes, frogs and reptiles, entirely new species are described almost every year and many new taxa await description. The description of new species of birds or mammals occurs less frequently. However, many taxa among these high-profile groups have not yet been subject to careful morphological analysis or any form of molecular genetic assessment. More

often than not, the results of such studies challenge traditional taxonomies based on morphological or field studies, and there are many examples where molecular genetic studies have revealed additional complexity in what were thought to be well-studied taxa.

At a finer level of analysis, patterns of geographic variation have been investigated in a fair proportion of bird species and in a few fish, reptile and mammal species. Geographically isolated 'races' are commonly treated as subspecies, although the value of such usage has been variably contested and defended. Only very rarely is existing subspecies nomenclature based on a combination of morphological and molecular genetic data.

But the description of new species and finer discrimination of patterns of geographic variation are not the only reasons why the checklists presented in this volume are certain to undergo future modifications. As any reader of the journal *Systematic Biology* would appreciate, the science of classification itself is in a process of constant review and change, with significant debate at present over theoretical and practical aspects of 'species' concepts and methods of phylogenetic reconstruction, and even over our system of classification itself. These issues are not purely 'academic', but rather have a very direct impact on practical taxonomy, especially as it is mediated by the process of peer-reviewed publication. Several critical issues will be discussed briefly below as a means of introducing our own approach in compiling this checklist.

Species Concepts: in theory and in practice

The concept of a 'species' is so fundamental to biology that it almost seems ludicrous that it needs to be discussed. However, as will become evident from even a brief foray into the vast and ever-growing literature on species concepts, the issue embodies a suite of controversial issues at various levels ranging from the philosophical to the practical [see Claridge *et al.* (1997) and Wilson (1999) for a broad variety of approaches]. Here we will limit our discussion to the more practical application of species delineation as it pertains to vertebrate species, the great majority of which are sexually reproducing [see Echelle (1990) for an introduction to the taxonomy of 'clonally' reproducing vertebrates].

Much debate in the past has been concerned with the question of whether the species category is a 'real' as against an arbitrary unit of classification (e.g., Reippel, 1986; Kluge, 1990). Today, most theoretical taxonomists find it useful to think of species as 'individuals' rather than 'classes', which means that they are self-delimiting and independent of human perception. Another important attribute of 'individuals' is that they are

historical entities, with a distinct time and place of origin and of demise, and a unique history that sets them apart from other related individuals. Admittedly, these are abstract notions, but they serve to establish a theoretical framework within which to formulate more practical taxonomic procedures.

At the practical level, it is useful to consider two different biological scenarios – one in which a number of species are found living together (i.e., found in sympatry); and another where the various species do not overlap in geographic range (i.e., allopatric distributions). The former case is by far the simplest scenario in which to make objective taxonomic decisions.

Where two or more species live in a mixed community, they are generally provided with opportunities to interbreed. If they are sufficiently different in reproductive behaviour or anatomy or general ecology (collectively known as 'pre-mating isolating mechanisms'), there may be few actual attempts to interbreed and hence, little or no sharing of genetic material. However, even where mating does occur, the contributed genetic materials may differ in ways that either preclude its successful recombination, or else lead to a breakdown of embryological development or practices of parental care (collectively termed 'post-mating isolating mechanisms').

Where the various potential isolating mechanisms do not prevent interbreeding and successful reproduction, the resultant transfer of genetic material will tend to very quickly eliminate any genetic and morphological differences that might have existed between sub-populations. Conversely, to find differences either in genetic properties or in genetically-determined morphology between co-occurring or sympatric populations constitutes very strong evidence of separate species. This is of course the basis of the traditional 'Biological Species Concept' (BSC), first explicitly formulated by Dobzhansky (1937) and Mayr (1942) and since followed by the majority of animal taxonomists.

Traditionally, the recognition of sympatric species depended on the ability of a taxonomist to detect sometimes subtle differences in morphology or behaviour. These days, such decisions are more commonly made with reference to molecular genetic markers, resulting in vastly improved levels of both objectivity and certainty. Typically, a suspicion of sympatric species, aroused by morphological studies, is then either confirmed or refuted by analysis of genetic markers that effectively test the null hypothesis that all individuals in the combined population form a single reproductive pool. Recent case studies involving Western Australian vertebrates include Aplin and Adams (1998) and Donnellan *et al.* (2000).

Where groups of closely-related forms have non-

overlapping distributions, the opportunities to interbreed are rare to non-existent. Application of the Biological Species Concept in such cases thus requires the taxonomist to enter the realm of the hypothetical; specifically, to assess the likelihood that successful interbreeding would occur if members of two geographically-isolated populations were brought together under natural conditions. Ideally, such decisions would be based on detailed knowledge of pre- and post-mating isolating mechanisms in the group in question. In practice, such information is rarely available, and most taxonomic decisions are based instead on such subjective procedures as comparing degrees of morphological divergence.

Widespread dissatisfaction with the Biological Species Concept, especially as it pertains to the problem of allopatric populations, has resulted in a plethora of theoretical and practical contributions on the subject of alternative Species Concepts (see Avise and Ball 1990, Frost and Hillis 1990; Mallett 1995 for useful reviews). Here we will examine the implications of what is emerging as the dominant new paradigm – the Phylogenetic Species Concept (PSC).

The fundamental tenet of the PSC is that species-level units should equate to discrete evolutionary lineages (Nixon and Wheeler 1990; Baum 1992). In genera containing relatively few, well-differentiated species, this condition is easily satisfied. However, problems arise where a widely distributed taxon has given rise to distinctive local offshoots; in such cases the 'parent' taxon would be paraphyletic if it contained only some of its derivative lineages. This situation may actually be quite common in Australia, where many species have probably undergone major expansions and contractions in range in response to environmental change, and where there are many examples of species-groups comprising one or two widely-distributed taxa together with variable numbers of locally restricted endemics (e.g., the *Lerista nichollsi* species-group of skinks).

At the operational level, the PSC defines species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler 1990: 218; see also Davis and Nixon 1992). A species classification based on this principle would equate to the terminal nodes on a cladogram, thereby effecting a closer integration of phylogenetic theory and practice. However, for most groups of organisms, practical application of this principle would lead to a very significant increase in the number of species, including elevation of virtually all populations currently identified as subspecies to full species level. A good example is Cracraft's (1992) phylogenetic classification of the Birds-of-

Paradise in which he recognized a total of 90 species compared with the 40–42 listed by classical taxonomists such as Mayr (1962) and Gilliard (1969).

Even more problematic, however, is the potential for the increasingly sensitive techniques of molecular genetics to diagnose extremely transitory and/or local populations (e.g., demes or peripheral populations based on small founder groups), irrespective of the degree of divergence in morphology or general biology. For example, under the PSC, various isolated populations of each of the endemic southwestern Australia frog species, *Geocrinia rosea*, *G. lutea* and *G. alba*, could be diagnosed as a distinct species based on fixed allelic differences (Driscoll 1998a, 1998b). The solution, of course, is for the PSC to be applied within the context of metapopulation theory (Hanski and Gilpin 1998), thereby making allowance for differences in demographic structure, population dynamics and levels of genetic variability; however, what might be lost is the essential (or perhaps naive) simplicity of the PSC as it exists today.

Not surprisingly, the Phylogenetic Species Concept has thus far failed to bring about widespread changes in taxonomic practice. Nevertheless, it is interesting to note an increasing frequency of mention of the PSC in the context of recent systematic revisions, and a growing emphasis on its key elements of monophyly and diagnosability. Schodde and Mason (1999), for example, in their recent classification of Australian birds, refrained from employing the PSC, but instead introduced a new concept, the 'Ultrataxon', defined as "regional inter-breeding populations of birds that differ discontinuously from neighbouring relatives in at least one morphological character that is presumed to be genetically based" (Schodde and Mason, 1999: 4). The resultant 'ultrataxa' are in reality equivalent to monotypic species or to subspecies where significant regional differentiation is present, and also correspond to 'terminal taxa' or Phylogenetic Species in the sense of Nixon and Wheeler (1988). The only real advantages of the 'ultrataxon' label are therefore to avoid the "stigma attached to 'subspecies' in conservation biology and elsewhere" (Schodde and Mason, 1999: 3), and to avoid "ambiguity and confusion in classification" through contrasting usage of the term 'species'. In Schodde and Mason's system, the term 'species' is retained for the larger evolutionary units that are believed to have attained the state of reproductive incompatibility; i.e., Biological Species *sensu* Mayr.

For the present checklists, we have retained the more traditional use of species and subspecies. In broad terms, these categories are employed in the sense of the conceptual paradigm of the BSC, that is species are essentially biological entities maintained by *intrinsic* attributes promoting reproductive

isolation, while subspecies are essentially geographic entities maintained by *extrinsic* factors that effectively deny reproductive interaction. Under this definition, the recognition of subspecies within a species will generally indicate the existence of morphologically-diagnosable populations in strict allopatry. Where closely-related taxa are in narrow contact and show evidence of hybrid activity, the decision to recognize the forms as species or subspecies generally rests on evidence regarding the frequency and spatial scale of hybridization and the extent of introgression. At one extreme, occasional or spatially restricted hybridization with limited introgression generally has little impact on the separate identity of populations. On the other hand, frequent, widespread hybridization and effective introgression is likely to eliminate genetic and morphological distinction in only a few generations.

Wherever possible, we have eliminated any prior subspecific nomenclature that has existed solely to signify geographical isolates in the absence of morphological or other differentiation, or to designate subdivisions or points along extended clines. Both practices were of course standard practice during the earlier years of systematics in Australia, as elsewhere in the world (Wilson and Brown 1953).

Exactly how these taxonomic principles are applied in practice depends on what kinds of evidence are available for any group of animals. Under ideal circumstances taxonomic assessments should be based on a combination of molecular genetic, ecological and ethological, and morphological evidence. However, this ideal is only rarely attained, and many decisions are thus made in the absence of critical evidence. In such cases, some ranking of evidence is probably advisable to assess the potential stability of any decision.

In many respects, molecular genetic evidence provides the most direct evidence on which to base taxonomic decisions. The level of genetic divergence, as measured by allozyme electrophoresis, directly measures the extent of gene flow between populations. As noted earlier, this can provide a powerful test to either confirm or refute the existence of two or more morphologically-similar species in sympatry. In the case of allopatric populations, the level of genetic divergence can be used to estimate the extent of contemporary gene flow and, provided something is known of the population dynamics and demography of the organism, to estimate the approximate duration of isolation between the gene pools (expressed in terms of generations). However, a more frequently-used approach is to compare patterns of genetic differentiation *within* and *between* populations. Georges and Adams (1996: 251), for example, noted that "the four fixed differences between *Elseya*

latisternum and the undescribed form of *Elseya* from the Gwydir River ... stands in stark contrast to the absence of fixed differences among populations of *Elseya latisternum* ranging from the Richmond River in NSW to Cape York and Arnhem Land".

At a broader comparative level, there is also a wealth of empirical evidence to suggest that certain levels of genetic divergence (as measured by allozyme electrophoresis) are associated with the attainment of reproductive isolation. Thorpe (1982) for example, found that among non-avian vertebrates, 97% of published interspecific comparisons gave Nei's D in excess of 0.16. Avise (1975) reported similar figures among the majority of groups of birds, but with consistently lower values in certain families. However, in all groups investigated, the data show a broad overlap of values between intraspecific and interspecific contrasts, therefore negating the use of a genetic 'yardstick', even within a single group.

Recent developments in the field of molecular systematics have also provided a new tool for taxonomy in the form of maternally-inherited mitochondrial gene trees. By combining information from two or more such trees, the pattern of historical descent of individuals and populations can be reconstructed with a high degree of confidence. This approach is particularly important in the context of the Phylogenetic Species Concept, as it can potentially distinguish monophyletic from non-monophyletic (para- or polyphyletic) taxa. Sibling species recognised under the PSC are expected to satisfy the criterion of reciprocal monophyly. A combined analysis using allozyme electrophoresis and some form of mitochondrial DNA analysis is likely to provide the best estimate of population phylogeny and hence the most reliable and stable species-level taxonomy.

Perhaps the next most useful body of taxonomic information is represented by components of what Paterson (1980, 1985) termed the 'Specific Mate Recognition System' (SMRS)—the suite of ethological, anatomical and biochemical attributes that together serve to establish a distinction between more and less appropriate mating partners and thereby limit the field for potential genetic recombination. The SMRS can include advertisement calls, pheromones, sexual displays, details of reproductive anatomy etc., all of which are potentially under strong sexual selection and thus capable of very rapid divergence (Arnold 1986; Turner and Burrows 1995). At the practical level, taxa which differ in one or more key components of the SMRS can probably be assumed to have attained a significant level of reproductive incompatibility under natural conditions.

The extent of general morphological divergence between populations, despite being the traditional

basis for most original species descriptions, in reality provides the least satisfactory basis for taxonomic ranking. In several well-studied groups of vertebrates, there is strong evidence for significant morphological sub-division *within* panmictic species, and conversely, for the attainment of reproductive incompatibility in the absence of significant morphological divergence (e.g., Larson 1989). Particular caution must be exercised where putative taxa are based on patterns of geographic distribution of one or a small number of morphological characters, especially where such characters may represent the expression of one or a few genetic loci. In such cases, there is a clear danger that the resultant taxonomy is in fact a typological construct based on a pattern of selection or drift operating on a few loci, and non-representative of patterns of variation in other, possibly less visible, but in a taxonomic sense, no less significant, genetic loci.

In concluding this discussion of species-level classification it is also worth noting that the most completely-investigated examples of species radiations, incorporating a variety of different lines of molecular and morphological evidence, rarely ever result in unambiguous, hierarchical taxonomies. The reason for this is that intra-specific evolutionary processes, operating at the level of the deme or avatar (*sensu* Damuth 1985), are intrinsically reticulate in nature, and are therefore incompatible with the simple models of cladogenesis that are encapsulated within our hierarchical Linnean system of classification. As a general rule of thumb, the more we learn about the evolutionary history of a group of related species, the less likely we are to be able to express those relationships via standard taxonomic conventions.

The meaning of higher categories: genera, families etc.

Traditional arrangements of species into genera and families were often essentially typological, a simple bringing together of groups of species on the basis of general similarity. In some cases, this resulted in natural evolutionary groups, but more often the groupings were based on suites of shared primitive features or common ecological adaptations.

Today, most taxonomists agree that systems of classification above the species-level should attempt to reflect the evolutionary relationships of the individual species. While this is a laudable goal, for many groups of organisms, it remains a tall order. Among the various groups of Australian vertebrates, knowledge of even the most basic anatomical systems (e.g., skeletal anatomy) is usually far from complete, and while a rapid growth in the number of molecular studies is leading to improved phylogenetic knowledge in

many groups, these studies are often based on only a few members of any group.

For a group of animals where much of the phylogenetic information is very patchy in coverage, the dilemma for the taxonomist is to know just when to recommend taxonomic changes. If changes are made prematurely and on the basis of inadequate evidence, they generally require subsequent modifications, creating a plethora of short-lived combinations that mar the taxonomic literature and serve only to alienate non-taxonomists. On the other hand, conserving traditional generic and familial classification for the sake of taxonomic stability, even when it is clearly contradicted by a significant body of phylogenetic evidence, is also potentially counter-productive. This is because taxonomy is far more than a passive system of names; rather, as emphasised earlier, it plays an active role in guiding the selection of species in comparative research, and more critically, in the setting of priorities for species conservation. For these reasons, it is important that classifications are able to change to reflect genuine improvements in phylogenetic knowledge.

The conflicting need for stability and change has prompted some contemporary taxonomists to champion a dual system of taxonomy – one set of unchanging names to identify species units; and a second system for expressing the phylogenetic relationships among the fundamental species units (de Queiroz and Gauthier 1992; Cantino *et al.* 1999). Although such suggestions seem overly radical to many taxonomists, they are likely to gain much support from other biologists for whom the most pressing need is to unambiguously label a particular organism and to identify other information pertaining to the same organism. However, pending further development of such alternative systems of classification, there is a continuing need for conventional taxonomic revision.

In the present lists, generic and higher taxonomic groupings are based on our best estimate of the phylogenetic relationships of the included taxa, based on both published works and our own unpublished studies. In cases where these relationships are unclear, we have generally adopted a conservative position by grouping taxa in a way that maximizes the number of monophyletic taxa, but avoids any arbitrary subdivision of taxa of uncertain phylogenetic structure.

Style and content of the individual checklists

Each of the individual checklists differ slightly in style and content. To a large extent this reflects differences in the state of taxonomic and phylogenetic knowledge of each group of vertebrates. However, it also reflects differences in

the practical application of taxonomic conventions among animal taxonomists.

The major difference between the checklists relates to the number of categorical ranks employed and the ordering or 'sequence' of taxa. For the fishes, taxa are grouped only at familial level, with the families arranged and numbered according to a standard convention that approximates the higher level phylogenetic relationships. In the mammal checklist the taxa are grouped at three categorical levels only (family, order and subclass) and are listed in alphabetic order at and below each of these levels (ie families within orders; genera within families; species within genera). The checklist of reptiles and frogs employs a larger number of categorical ranks but otherwise maintains alphabetic listing at and below each level. Finally, the checklist of birds employs an expanded number of categorical ranks together with an arrangement of all taxa according to a 'phylogenetic sequence' incorporating information both as to the degree of relatedness and the relative primitiveness or degree of specialization of the various taxa. The value of this approach has been defended recently by Schodde and Mason (1999: 5).

Common or vernacular names

Common or vernacular names are provided only for those groups where there is an established usage (e.g., for birds and mammals). In some cases, several common names are given, reflecting a lack of uniformity in current usage and the absence of any universally-accepted criteria for choosing between alternatives. Common names are not governed by any international code of nomenclature equivalent to that in use for scientific names, although there is a growing push from certain quarters (especially among ornithologists) toward institutionalisation of 'English' names.

Many taxa, especially among the reptiles and fishes, currently do not have any 'common' name. In most cases they probably do not need one, as they are rarely ever seen and even less often discussed outside of the scientific literature. In these cases, it is our opinion that common names are best left to emerge rather than being imposed in an arbitrary manner for the sake of completeness or uniformity.

REFERENCES

- Aplin, K.P. and Adams, M. (1998). Morphological and genetic discrimination of new species and subspecies of gekkonid and scincid lizards (Squamata: Lacertilia) from the Carnarvon Basin region of Western Australia. *Journal of the Royal Society of Western Australia* 81: 201-223.
- Arnold, E.N. (1986). The hemipenis of lacertid lizards (Reptilia: Lacertidae): structure, variation and systematic implications. *Journal of Natural History* 20: 1221-1257.
- Avise, J.C. and Ball, R.M. (1990). Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surveys in Evolutionary Biology* 7: 45-67.
- Baum, D. (1992). Phylogenetic species concepts. *Trends in Ecology and Evolution* 7: 1-2.
- Cantino, P.D., Bryant, H.N., de Queiroz, K., Donoghue, M.J., Eriksson, T., Hillis, D.M. and Lee, M.S.Y. (1999). Species names in phylogenetic nomenclature. *Systematic Biology* 48: 790-807.
- Claridge, M.F., Dawah, H.A. and Wilson, M.R. (eds) (1997). *Species: the units of biodiversity*. Chapman and Hall, New York.
- Cracraft, J. (1992). The species of the Birds-of-Paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. *Cladistics* 8: 1-43.
- Damath, J. (1985). Selection among "species": a formulation in terms of natural functional units. *Evolution* 39: 1132-1146.
- Davis, J.I. and Nixon, K.C. (1992). Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic Biology* 41: 421-435.
- De Queiroz, K. and Gauthier, J. (1994). Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 7: 27-31.
- Dobzhansky, T. (1937). *Genetics and the Origin of Species*. Columbia University Press, New York.
- Donnellan, S.C., Aplin, K.P. and Dempsey, P.J. (2000). Genetic and morphological variation in Australian *Christinus* (Squamata: Gekkonidae): preliminary overview with recognition of a cryptic species on the Nullarbor Plain. *Australian Journal of Zoology* 48: 289-315.
- Driscoll, D.A. (1998a). Genetic structure, metapopulation processes and evolution influence the conservation strategies for two endangered frog species. *Biological Conservation* 83: 43-54.
- Driscoll, D.A. (1998b). Genetic structure of the frogs *Geocrinia lutea* and *Geocrinia rosea* reflects extreme population divergence and range changes, not dispersal barriers. *Evolution* 52: 1147-1157.
- Echelle, A.A. (1990). Nomenclature and non-mendelian ("clonal") vertebrates. *Systematic Zoology* 39: 70-78.
- Frost, D.R. and Hillis, D.M. (1990). Species in concept and practice: Herpetological applications. *Herpetologica* 46: 87-104.
- Georges, A. and Adams, M. (1996). Electrophoretic delineation of species boundaries within the short-necked freshwater turtles of Australia (Testudines: Chelidae). *Zoological Journal of the Linnean Society London* 118: 241-260.
- Gilliard, E.T. (1969). *Birds of Paradise and Bower Birds*. Weidenfeld and Nicholson, London.
- Hanski, I.A. and Gilpin, M.E. (eds) (1998). *Metapopulation Biology*. Academic Press, New York.
- Kluge, A.G. (1990). Species as historical individuals. *Biology and Philosophy* 5: 417-431.
- Larson, A. (1989). The relationship between speciation and morphological evolution. In D. Otte and J.A.

- Endler (eds), *Speciation and Its Consequences*: 579–598. Sinauer, Sunderland, Massachusetts.
- Mallett, J. (1995). A species definition for the Modern Synthesis. *Trends in Ecology and Evolution* 10: 294–299.
- Mayr, E. (1942). *Systematics and the Origin of Species*. Columbia University Press, New York.
- Nixon, K. C. and Wheeler, Q. D. (1990). An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.
- Paterson, H. E. H. (1980) A comment on “mate recognition systems”. *Evolution* 34: 330–331.
- Paterson, H. E. H. (1985). The recognition concept of species. In E. S. Vrba (ed.), *Species and Speciation*: 21–29. Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria.
- Reippel, O. (1986). Species are individuals: a review and critique of the argument. *Evolutionary Biology* 20: 283–317.
- Schodde, R. and Mason, I.J. (1999). *The Directory of Australian Birds. Passerines*. CSIRO Publishing, Collingwood, Victoria.
- Turner, G.F. and Burrows, M.T. (1995). A model of sympatric speciation by sexual selection. *Proceedings of the Royal Society, London B* 260: 287–292.
- Wilson, R.A. (ed.) (1999). *Species: New interdisciplinary essays*. MIT Press, Cambridge, Massachusetts.