I.
THE ANTIQUITY OF THE SOUTHERN TEMPERATE AVIFAUNA

In a recent taxonomic review of South Australian birds the writer (1951) found that a high percentage of land birds resident in the Mount Lofty highlands and vicinity were not racially separable from populations in the more humid or highland regions of south-eastern Australia although separated from them by an area of many hundreds of square miles of semi-arid scrub country which contains a distinct avifauna of its own.

The following are some of the species concerned: Swamp Parrot (Pezoporus wallicus)—recorded from the Adelaide Plains and Mount Compass district (now extinct, both places); lingers in the South-East of South Australia and restricted areas eastwards. Glossy Black Cockatoo (Calyptorhynchus lathami)—a small population of probably less than fifty birds on Kangaroo Island; once occurred in the Mount Lofty Ranges, but now mainly in coastal New South Wales. Painted Quail (Turnix varia varia). Brown Thornbill (Acanthiza pusilla macularia). Yellow-tailed Thornbill (A. chrysorrhoa sandlandi). Striated Thornbill (A. lineata chandleri) (on Kangaroo Island only). Chestnut-tailed Ground Wren (Hylacola pyrrhopygia subsp.)—resembles Victorian birds closely. Spotted Quail-Thrush (Cinclosoma punctatum). Ground Thrush (Turdus dauma). Eastern Spinebill (Acanthorhynchus tenuirostris). Regent Honeyeater (Zanthomiza phrygia). Yellow-faced Honeyeater (Meliphaga chrysops). Crescent Honeyeater (Phylidonyris pyrrhoptera). Noisy Miner (Myzithra melanochepala). Beautiful Firetail (Zonaginthis bellus). Red-browed Finch (Estrilda temporalis).

The following species also demonstrate the close affinities of birds of the more humid parts of South Aus. with those of south-eastern Australia: White-browed Scrub-Wren (Sericornis frontalis rosinae)—this South Australian race is close to eastern birds (which are sometimes separated under the name longirostris). Striated Field-Wren (Calamanthus juliginosus)—there appears to be an unbroken clinal sequence from the Adelaide area to Victoria and Tasmania. Superb Blue Wren (Malurus cyaneus)—the race australis extends from southern New South Wales and Victoria as far west as Kangaroo Island and the Mt. Lofty Ranges to the Port Lincoln
area, and there is also a relatively isolated population along the River Murray. As far as South Australia is concerned all these forms are relicts.

Zoogeographically the Mt. Lofty Ranges may be regarded as an outlier or relict province of the humidity-loving avifauna which is believed to have extended across southern Australia in the more geologically recent past, and which now persists most strongly in the south-eastern highlands and Tasmania and less strongly in south-west Australia. The inhabitants of the dwarf eucalypt woodlands which separate the mainland areas are arid forms which must be comparatively recent arrivals following the replacement of humid habitats (and biotas) by drier ones. While it is possible that a few species may have bridged the gap lately between Victoria and South Australia, it is an inescapable conclusion that many birds with very local habits, in the South Australian highlands must have become cut-off from the eastern populations since the last glacial interval of the Pleistocene.

The climatic history of the Quaternary (Pleistocene and Recent epochs), although it has not been worked out in detail for Australia, is comparatively well-known, and its vicissitudes have been described by such authors as Zeuner (1945, 1946), Keble (1947), Tindale (1947, 1949), and Mayr (1950). The Pleistocene, which began not earlier than one million years ago, was characterised by alternations of glacial (cold, wet) and interglacial (warmer, drier) climates when owing to fluctuations of the amount of solar radiation there was a wide range of temperature between the maxima of glacial and interglacial interludes.

These climatic changes are believed to have resulted in a shift of the moisture zones in Australia with corresponding movements of the biotas. During glacial periods the centre of aridity would have been at a lower latitude than at present, with a marked extension of the humid zones in the southern half of the continent. Lake Eyre would have again become the centre of a vast fertile area as it was in earlier time in the Tertiary. In the interglacials somewhat less pluvial conditions may have prevailed in the south and the centre of aridity would have moved to a higher latitude with Lake Eyre in the arid belt. Owing to the rhythmical nature of these fluctuations it is conceivable that a region would have passed successively from desert into savanna or savanna into wet forest, to revert later to a former condition.

According to Zeuner several pairs of wet and dry phases occurred in Europe during the last 600,000 years, and an attempt has been made to correlate Australian data with these by Tindale (1947). Reference to the Table supplied by Tindale suggests that resident subspecies in the South Australian highlands must have endured without change since the end of the last Pleistocene glacial interval (Wurm—stage III), involving a period of perhaps 22,000 years. Assuming that these races once extended right across south-eastern Australia as far west as the Mount Lofty Ranges in more pluvial times, the latest period under which such conditions occurred was about 23,000 years ago. With the contraction of the range of the humid races, well-differentiated eremic types moved in, so that both groups must have already been in existence. It has been estimated that the Wurm glacial, of which three stages are recognisable, may have commenced about 115,000 years ago and lasted for 92,000 years. There appear to have been one or two mild or temperate interstadials of negligible importance and duration during this time. Possibly the present day humid forms were differentiated much earlier. Tindale (1949) has suggested that the climate in post-Pleistocene times (10-20,000 years) in southern Australia at least has been slowly deteriorating from one of pluvial conditions and that the climate has never been much drier than at present during the Quaternary. Earlier glacial stages during the Pleistocene, with an average duration of little more than 40,000 years each, were separated by interglacials of longer duration (60,000 and 190,000 years), but it is believed that conditions were relatively mild and rainfall probably plentiful throughout. (Hills, 1939; Whitehouse, 1940; Crocker and Wood, 1947). In other words, the general climate was probably more stable in Australia than might appear at first sight. Serventy (1953) has postulated a Pleistocene origin for a number of genera, species and subspecies but, even allowing for different evolutionary rates, owing to the relatively short time involved during climatic phases it seems preferable to regard the Quaternary climatic fluctuations
as responsible mainly for infra-specific variation. While the intensity of the interglacial periods remains problematical, it is possible that they had little effect on the avifauna in the south-eastern humid belt apart from a restriction of available habitats which again became available in more pluvial times.

It is thought that the Early Pleistocene and Upper Pliocene in Australia may have had a climate very similar to that of to-day, although the humid zones may have been wider and the desert regions were much restricted. Possibly the eremic fauna was initiated or considerably enlarged at this time, new species arising by re-adaptation of some populations which had been integral parts of the old humid fauna. How this occurred is not known, but from present distribution of the younger members of the eremic group it might be suggested that natural selection was a primary factor and that gene flow between neighboring “wet” and “dry” country populations was, and has continued to be, of minor influence. Mayr (1949) refers briefly to this question in connection with other matters and quotes Dobzhansky (1947) who found that the selection coefficient in wild populations of Drosophila was unexpectedly high. Thus a simple shift in the position of a single gene could be far-reaching and remarkably advantageous to an organism meeting the stress of changing environmental conditions.

It is known from geological evidence that southern Australia, especially the south-eastern portion, has consistently enjoyed rather genial conditions for a considerable period of time—probably since the beginning of the Tertiary—with only slight recessions. Numerous endemic families and genera of birds derived from early subtropical biotas gave rise to the very distinctive faunal suite now found in the south-east and traces of which linger in parts of South Australia and Western Australia. The period of evolution was perhaps 60 million years or more, and suggests that some of the elements of which it is composed may be of great age even at the specific level. The oldest endemics according to Mayr (1944, 1951) include members of the parrot-tribe, such as the cockatoos and broadtails, the lyrebirds, scrub-birds and honeyeaters, and a few others. The strong ecological preferences exhibited by some of these suggests that the adjustment of their physical and psychic requirements occurred long ago and that certain genera developed rather slowly in the more or less continuously available humid climates of the Tertiary and that their arid country representatives are comparatively recent adaptations. The mud-nest building habits of the Magpie-Lark (Grallina), Apostle-bird (Struthidea), and the Chough (Corcorax) may be an indication that these species arose in a moist climate rather than any very close taxonomic relationship. Nevertheless, they may be more closely related to one another than was thought at one time (cf. Amadon, 1950; Beecher, 1953).

The antiquity of birds is great and the magnitude of the period of evolution is of the order of 140 million years. It is important to remember that very little is known of avian history during the first half of this vast span of time. After the first 80 million years, at the beginning of the Tertiary, birds had reached their maximum abundance as a class and most of the orders known to-day were already differentiated. From this time onward, although the evolutionary rate must have slowed down considerably, birds became progressively more modern in structure and appearance, and Wetmore (1951) is of the opinion that “our living kinds had their evolution, both as genera and species in the Miocene and Pliocene ... ” If Wetmore’s assertion is applicable to Australian birds, and there seems no reason to think otherwise, then the question of the origin of present-day forms is shrouded in the little known happenings of many millions of years ago.

According to Mayr (1944, 1951), a group of old endemic families (about 14 in number) which show no close affinities with similar birds in any other particular region probably arrived in Australia no later than earliest Tertiary times, perhaps 60 million years ago. Although Australia was virtually isolated very early in the history of birds, certain groups continued to enter the continent from time to time, and in the papers already referred to Mayr has traced by indirect methods the numerous incursions from Asia through the ages up to Late Pleistocene and Recent times. He concluded “... the fauna of Australia is ... composed of layers of elements that show closer and closer relationships to the Asiatic fauna.” There is much evidence to indicate that the great land
mass of Asia formed a “cross-roads” or else was the centre whence various animal stocks originated and migrated to other parts of the world, and most biologists now agree that the islands to the north of Australia provided a means of entry for a large part of our fauna since the end of Mesozoic times.

Nevertheless a large part of the avifauna must have arisen in isolation during the greater part of the Tertiary period in the Australian continent when it was finally separated from Asia by an archipelago which is believed to have changed little in character right up to the present. The ability of some groups and genera to retain their basic characteristics for many millions of years leads one to assume that in Australia many of the older endemic families may still resemble closely their ancient forebears. Living conditions in the Early Tertiary are believed to have been very different from those of to-day.

On meteorological grounds it is thought that the climatic zones followed their present sequence, but from remains of rain-forest types and open forest elements found in the floras of freshwater beds it would seem that the warmer zones were wider than at present and that Australia south of the Tropic and including Tasmania enjoyed a very humid climate. Owing to the moist conditions, lowland floras would have predominated and deserts may have been unknown. Gould (1940) has suggested that a pre-requisite to glaciation in Antarctica (which he believes began in the Middle Tertiary) would have been humid climatic conditions in the southern hemisphere.

In later Tertiary times, when extensive transgressions of the sea in the west and south occurred and tectonic uplift commenced, geological evidence has indicated a contraction of the humid forests and the development of temperate forests in the south.

The first major rift between the northern and southern elements of the old avifauna probably occurred now following the appearance of drier or even desert conditions on a minor scale in the centre of the continent in the late Miocene or early Pliocene. About this time or earlier the considerable encroachment of the seas in the Nullarbor region and the formation of the Adelaide and Murravian gulfs would have caused another rift between east and west, and the influence of these barriers is perhaps reflected to-day in the occurrence of certain species in southern Australia.

By the close of the Tertiary it seems likely that the three main groups of modern bird species (or avifaunas) were recognisable. The ancient biota which gave rise to the southern temperate avifauna was probably once characteristic of a major part of the continent. It also spread to New Guinea and traces are evident in New Zealand and adjacent islands. Its dismemberment began as a result of climatic changes during the Tertiary, and clearly these stresses which also gave rise to the present eremic avifauna are still in operation. Increasing land relief towards the close of the Pliocene enabled certain ancient types to persist in restricted marginal areas.

Nothing is known of deserts in Australia in the earlier Tertiary, and whilst many authors consider that they have always existed, though their position and extent may have varied, Axelrod (1950) believes that desert environments are phenomena of latest Cainozoic time and first appeared in the Pliocene. The status of the eremic fauna suggests that it has evolved steadily at least since the beginning of that epoch, new forms mainly derived from the southern temperate fauna being incorporated in it from time to time. Some of our oldest desert species could be at least eleven million years old, while others appear to be much younger. Undoubtedly the marked “break” between the tropical, temperate, and eremic avifaunas is governed by ecological requirements and largely dependent on the adaptations of the species concerned, which leads one to believe that the various forms must have arisen in different climatic zones and that the latest changes in climate since the Pliocene or Pleistocene have been responsible for the fragmentation of many species with limited tolerances and the expansion of others. By their distribution many forms seem to show their common origin and in certain instances it is obvious that the species of to-day are the subspecies of “yesterday.”

The occurrence of most species tends to be limited by their ecological conservatism, but once having conquered a new environ-
ment further evolution may take place, and in South-West Australia the remnants of the old southern fauna are becoming adjusted to the more arid conditions of the present. Serventy and Whittell (1951) suggest that the south-western forms may have been cut-off not only by a contraction of the humid belt in southern Australia, but also quote Fairbridge in stating that another factor could have been the formation of the Great Australian Bight by down-faulting in the late Pliocene or early Pleistocene. This would point to a great age for the species concerned as well as a relatively slow evolutionary tempo in most forms. However, a number of south-western forms show differences at the subspecific level which could mean that separation finally occurred some time during the Pleistocene.

The taxonomic status of the Western Magpie (Gymnorhina dorsalis) has recently been discussed by Amadon (1951, 1953), Storr (1952), and Serventy (1953). Present day distribution of the various forms of the genus indicates their common origin. The New Guinea race, G. tibicen papuana, is not very different from northern Australian birds, and this is an indication that the last land connection between that island and the Australian continent was comparatively recent and probably occurred towards the close of the last glacial interlude of the Pleistocene, some 23,000 years ago. “Black-backed” and “white-backed” magpies were already differentiated at this time. The magpies seem to have arisen as a small community of woodland savanna forms in the interior of the continent and became dispersed following increasing aridity, and the large northern tibicen s.l. and the diminutive Tasmanian hypoleuca s.str. may have been the end members of a once Australia-wide cline. The western dorsalis perhaps arose by “hybridisation” of black-backed and white-backed forms, following an early segregation of the latter. This is suggested by the rather variable nature of the black back in females of dorsalis even though the males are white-backed. Variation in this form, whilst not quite at the normal level, is approaching a stable condition.

In eastern Australia, inter-breeding of tibicen and leuconota occurs over a wide area, but owing to the great individual variation of “hybrids,” the zone of contact may be plotted only with difficulty. This secondary intergradation (Mayr, 1942) causes a progressive reduction in the width of the black saddle in “hybrids,” and being the only visible character by which such individuals may be recognised, its suppression might lead observers to assume that the “hybrid population” is unable to maintain itself. There is no evidence in support of this assumption, and there is little doubt that hybrid birds are numerous. Conspecificity of leuconota and tibicen is indicated. Serventy regards dorsalis and leuconota as conspecific and leuconota and tibicen as semispecies (i.e. allopatric species which have failed to achieve complete reproductive isolation). The present writer holds the view that all members of the genus belong to one species, tibicen, even though the various forms may be older than is thought usual for avian subspecies.

A “hybrid” origin could be postulated for the Adelaide Rosella, “Platycercus adelaidae,” which is sometimes regarded as a full species or else as a race of the Crimson Rosella, Platycercus elegans. Serventy, once an advocate of the latter view, now inclines to the former (1953). The taxonomic status of the rosellas in the Mount Lofty Ranges is complicated by the presence on Kangaroo Island of a bird which looks very like the eastern elegans superficially. It was named as a full species by North, who called it melanoptera on account of the greater amount of black on the shoulders. Although it is completely isolated geographically from the eastern populations of elegans, and therefore no inter-breeding is possible, no one to-day would consider it anything but a race of that form. The distribution can only be explained by the disappearance of a suitable habitat linking east and west. This may have occurred as late as 10,000 years ago and certainly not more than 20,000 years ago. The isolated occurrence of the Adelaide Rosella in the Mt. Lofty highlands and the Yellow Rosella (flaveolus) in the river-gums of the Murray and Darling must be due to the same happenings which were responsible for the separation of melanoptera.

As pointed out by the writer in 1941, there is a clinal sequence of three stages from a pale, yellowish race subadelaidae in the lower Flinders Ranges, through adelaidae in the Mt. Lofty Ranges, to a more reddish form...
flaurieuensis on Fleurieu Peninsula which is separated from Kangaroo Island by about 9 miles only at the narrowest point: Certain writers have attributed the "redness" of flaurieuensis to an infusion of "elegans-blood" from the Island. Whilst this might seem an obvious explanation, it is a remarkable fact that no trace of the heavier black shoulders of the Island race is apparent in Fleurieu birds. Lendon (1949) has stated that field observations have led him to believe that some individuals on Fleurieu Peninsula are no redder than birds further north. Numerous specimens examined or collected over a period of more than 20 years do not support this view, even in immature examples, and demonstrate the danger of relying on sight observations where color alone is involved. Actually individual variation in flaurieuensis is slight. The form adelaidae, which has the greatest geographical range in the cline series, is rather variable, but the characters of subadelaidae are less so and this race cannot be lumped with flaveolus as was done at one time. Contact between flaurieuensis, adelaidae, and subadelaidae is sharp. With flaveolus (the Yellow Rosella) it is a common belief that no secondary intergradation occurs and as noted by Serventy (1953) this is probably the case in eastern Australia perhaps owing to the fixation of slightly different habitat or ecological preferences. There are several skins in the South Australian Museum from west of Morgan, River Murray, which are paler than typical adelaidae, and perhaps intergradation or hybridisation in this region is more general than has been suspected. True adelaidae is found along the Burra Creek which enters the Murray River near Morgan, and this would provide opportunities for interbreeding. E. F. Boehm (1954), who has studied the birds of this district for many years, has expressed a similar opinion.

It is conceivable that elegans was originally the eastern (humid zone) red form, with flaveolus as an interior (sub-humid zone) yellow form, and that following the spread of the red form westwards in a more pluvial period, hybridisation between the two could have produced the rather variable "adelaidae-type" which became segregated in the Mt. Lofty highlands and further northwards, with some new genetic characters or combinations. "Pure" flaveolus, perhaps originally a denizen of more northerly latitudes, managed to survive in the Murray Valley, and melanoptera on Kangaroo Island.

There are other species with forms which parallel the distribution of Platycercus elegans on Kangaroo Island and south-eastern Australia. The insular races Acanthiza pusilla zietzi and Acanthiza lineta chandleri show close affinities with Victorian birds and the Glossy Black Cockeroo (Calyptrhynchus lathami), which is not on the adjacent mainland, is known from western Victoria. These occurrences point to the recent disappearance of connective populations.

Taijana, which has been colonised at different intervals by various species, seems to have been connected at its north-eastern end with the mainland during the Pleistocene and is known to have been part of the Australian continent in the earlier Tertiary.

The somewhat impoverished present-day fauna of this island is quite distinct and characterised by the much larger size of a number of birds and mammals with mainland relatives; others show no great differences, although an increase in pigmentation commonly occurs. At least half a dozen mammals are larger (and also darker) than mainland forms in accordance with Bergmann's rule (applicable to the higher vertebrates) which states that the correlation between geographical variation and temperature results in an increase in size in cooler climates. Of 187 land birds in Tasmania, about 35 are endemic forms, including nine species. There are also two endemic genera—Acanthornis and Amaurodryas—the latter being the only bird quoted by Baldwin Spencer (1896) as typical of his "Bassian region." More than twenty forms have relatives in south-eastern Australia and the Mt. Lofty highlands.

The large size of Tasman birds could be regarded as an extension of the size trend observable on the mainland, although the "break" is sometimes marked. The following are larger than mainland representatives: Tribonyx mortierii, Falco berigora tasmanica, Platycercus caledonicus, Pachycephala pectoralis glaucura, Colluricincla harmonica strigata, Calamanthus fuliginosus anthooides, Myzanza melanocephala leachi, Anthochaera paradoxa, Corvus coronoides tasmanica, Cracticus torquatus cinereus, and others.

Although an increase in size has been re-
corded from certain islands in various parts of the globe, no general explanation for the phenomenon is forthcoming, and often it is uncertain whether large island forms evolved locally, although this is generally assumed. In sympatric forms the older colonisers of islands tend to be larger, depending, of course, on the time interval between invasions and perhaps the degree of competition for food. The endemic Tasman species *Acanthiza ewingii*, now believed to be an early offshoot from *Acanthiza pusilla*, has the tail and tarsi longer but the bill shorter than the more recently-arrived, resident *Acanthiza pusilla diemenensis*. Perhaps by coincidence the average value of the tail/wing ratio of *ewingii* is approached most closely in the south-west Australian forms of *pusilla*—*apicalis* and *leuwinensis*—being 92-93 as compared with the values of eight other mainland races of *pusilla* which range from 80 to 89 (Mayr and Serventy, 1938). The race *zetzi*, from Kangaroo Island, which has an average tail/wing ratio value of between 89 and 90, may serve to link south-western and Tasmanian forms, a suggestion which is supported by its geographical location.

Although the evidence may not be regarded as completely satisfactory by some workers, the fossil *Tribonyx effluxus* which was described by Devis (1892) from the Pleistocene of Queensland was found to be large and about the size of the Tasmanian Native Hen, *Tribonyx mortieri*. Perhaps this Tasmanian species and other endemics have retained the tendency to grossness which was characteristic of many of the higher vertebrates known from the Pleistocene and which became extinct by the beginning of Recent times.

II.

THE "GREAT ARID" HYPOTHESIS AND REFUGE AREAS

One of the major problems of Australian ornithology is how speciation and phyletic divergence arose in the past, for on this question hinges the nomenclature of numerous birds whose taxonomic status is the subject of varied opinion. Geographic speciation on continents has been discussed by various authors in recent years (e.g. Mayr, 1950), and it is considered that the same processes which produce insular forms are universally operative. In other words, new subspecies and species arise following genetic changes induced by new conditions (and selective factors) during geographic isolation. On a continent like Australia, where sharp physical barriers such as water gaps and mountain chains have been limited, the required isolating barriers seem to have been provided by large areas of unfavorable terrain which appeared following fluctuations in climate and vegetational changes. Such conditions exist at the present time, and the inhabitants of the coastal humid belts are mainly relicts which enjoyed a greater range in the very recent past. The gradual, long-term process of extermination of the southern humid fauna worsened towards the end of the Pleistocene, and in South Australia such birds as the Glossy Black Cockatoo and Swamp Parrot (*Pezoporus*) are now near the point of extinction, whilst it is possible that ‘typical’ south-eastern species like the Spotted Quail Thrush (*Cinclodesoma*) and Superb Blue Wren (*Malurus cyaneus*) may have been “on the way out” before a fickle climate and that this process is now being aided by agricultural development and other man-made ecological changes. Under optimum conditions in the Pleistocene the humidity-loving groups would have been widespread, with imperfectly-isolated populations. The contraction of the original biotas of which they formed a part was a response to the secular changes which reached a climax towards the close of that epoch when an expansion of species with greater tolerance for aridity was accelerated also.

A number of writers, including Crocker and Wood (1947), Gentilli (1949) Chisholm (1951), and Serventy (1951, 1953), take the opposite view and believe that speciation generally has occurred only recently. In their search for effective isolating barriers which would have permitted speciation, they have adopted with enthusiasm the hypothesis that a period of “intense dessication” began in Australia some 9,000 years ago as a Post-Glacial event which continued with minor fluctuations for about 5,000 years (Crocker, 1941; Browne, 1945). Crocker later (1946) expressed the opinion that great aridity occurred “probably much less than 9,000 years ago.” In 1951, Serventy suggested a modification of the original hypothesis. He thought that there may have been “two
periods, and not one, of intense aridity in
sub-recent times each separated by more
humid conditions,” and based his opinion
on the relationships of certain species of the
genus *Malurus*. He believes that this sup­
posed happening caused widespread extinc­
tion of the bird fauna as well as other
animals and plants. Those species which
managed to survive were “squeezed into
various humidity refuges around the coast
and in the highlands of central Australia.”

Present day distribution is believed to be a
result of dispersal of newly-evolved races and
species by radiations from refuge centres
following an amelioration of climate during
the relatively brief period of about 5,000
years which would have been involved from
the ‘close’ of the “Great Arid” up to the
present. A similar idea is expressed by Mayr
(1951), who states that the “humid marginal
zone” or “humid belt” of Australia “is broad
in humid periods, but contracts into a few
coastal pockets at the height of an arid cycle.
These pockets serve then as refuges (Gen­
tilli, 1949) for the humidity-loving fauna and
flora, and distinct populations evolve in each
refuge.” Mayr also points out, however,
that “the exact dates of the recent pluvial
and arid periods in the tropics are equally
uncertain. Zoogeographers (Gentilli, 1949;
Mayr, 1950) and geologists agree that there
must have been a period of extreme drought
in the recent past of Australia, but the geolo­
gists wonder whether it was 6000 years ago
or as early as 150000 years ago. The avian
data suggest that an earlier date (at least
50000 years) is more likely.” There is little
doubt that the time interval since the “close”
of the supposed great arid cycle of Crocker
and others is altogether too short for pheno­
typic evolution to have proceeded very far,
even though the rate of evolution of a taxo­
nomic species may vary within fairly wide
limits in different groups.

Doubts as to the validity of the “Great
Arid” hypothesis were first raised by Tindale
(1947 a, b; 1949), who pointed out that the
occurrence of certain plants and animals is
in direct contradiction to the findings or in­
terpretations of Crocker, Wood, and others.
He suggested that the data employed by
Crocker for establishing the existence of a
former great arid interval (which was sup­
posed to have been followed by a “wet”
cycle) may be of a composite nature and
refer to one or more climatic phases of the
Pleistocene. Tindale believes that the imme­
diate past climatic history of southern Aus­
tralia has been one of increasing warmth.
He cites as an example of the effect of this
phenomenon on the fauna the present dis­
tribution of the Satyrid butterflies *Tisiphone
abeona*, *Heteronymphia penelope*, and
*Oreixenica kershawi*. Certain races of these
butterflies, which now occupy relict niches in
the South-East of South Australia and
western Victoria, have critical moisture and
temperature limits. Their nearest relatives
are 175 miles and more distant in southern
Victoria and in the Federal Capital Terri­
tory, and assuming a former continuous
distribution, which in this case appears to be
indisputable, one can only conclude that the
climate since the Last Glacial interval has
never been much drier than at present.

The distribution of the small passerine bird,
*Acanthiza iredalei*, Samphire Thornbill, lends
support to the view that conditions until
recently have been relatively moist, and that
present aridity is a late development. The
Samphire Thornbill is split up by taxono­
mists into three or four geographical races
(Mack, 1936; Mayr and Serventy, 1938;
Condon, 1951). All are ground-dwellers,
preferring samphire flats in damp locations,
mangrove areas, saltbush or bluebush in
regions of claypans and salt ‘lakes’, or skul­
ing in heathy situations in districts of greater
humidity. The race *iredalei*, which has the
widest distribution, ranges from coastal Mid­
west Australia through a restricted arid region
eastwards to the dry interior of South Aus­
tralia. Very similar to it, and occurring in
similar situations in the vicinity of the Flin­
ders Ranges and on the Olary Spur, is the
race *morgani*. From their peculiar occur­
rence, it would seem that these two forms
were originally denizens of the margins of
swamps and lakes and that they have man­
gaged to persist despite the drying up of the
extensive sheets of water which covered a
vast area in the inland until the end of
Pleistocene times or later.

The southern races, *rosinae* and *hedleyi*,
are sedentary forms which are completely
isolated from the interior populations and
from one another. The former occurs on
the coastal samphire flats from Port Brough­
ton to Price on Yorke Peninsula and along
the eastern shores of the Gulf of St. Vincent, south to about Osborne. *Hedleyi* occupies a wide area of heath country inland from about Meningie eastwards to the Little Desert, Victoria. The southern forms were once connected to the inland populations perhaps through suitable habitats along the margins of ancient southward-flowing rivers or streams in the Spencer-St. Vincent sunkland. It is unlikely that any of the forms of *Acanthiza irendalei* could have survived much drier conditions than obtain at present. The birds are local in their habits and their present occurrence can be explained hardly with reference to 'refuge areas.'

There seems to be little or no difference between refuge areas and relict provinces, although current usage of the term "refuge" implies concentration and crowding of species in restricted localities, which is difficult to imagine. In a relict province, that is, one which has undergone an actual reduction in size, the elimination of some resident forms as a result of worsening conditions and competition might permit the entry of a few species able to grasp new or unoccupied niches, but such areas to be effective would have to be large, if not numerous, owing to the number of favorable niches which would be required. Reference to present-day topography leads one to believe that this would have been unlikely, except perhaps in the region of the south-eastern highlands of Australia. The Gawler Ranges, quoted by botanists and others as a likely refuge area, seem especially unfavorable for this purpose, being of limited extent and relatively low altitude. During an arid interval the Mt. Lofty Ranges would also have been unable to support a greater variety of species than occurs at the present time.

A large portion of southern Australia has been over-run by arid types and the recent appearance of such birds as the Galah (*Kakatoe roseicapilla*) and Crested Pigeon (*Ocyphaps*) in the south would indicate that the process is not yet completed.

The Black-capped Sittella (*Neositta pileata*) is not a common bird in South Australia, and the presence of a sparsely breeding population, together with the fact that it is "very numerous" in South-west Australia (Serventy and Whittell, 1951), may mean that it is a late-comer in South Australia.

With regard to the evolution of the Sittellas, I find myself in general agreement with the conclusions of Mayr (1950, p. 290). McGill (1948) has proposed a New Guinea origin for the group, but it is possible that the Papuan tree-runners may have originally come from northern Australia. The fact that *Neositta* is absent from Tasmania seems to point to its comparatively recent arrival in the south. Doubtless the common ancestor of modern forms had an orange wing-bar, which is now retained in the southern races, 'lost' or obscured in New Guinea birds (*papuensis*, etc.), and white in northern Australian forms.

McGill's suggestion that the Sittellas have reached southern Australia through two dispersal lines—one westwards through *leucoptera* to *pileata*, and the other along eastern Australia— is feasible when it is remembered that expansions of the humid belt in southern Australia during the last epoch would have resulted in increased aridity and a contraction of humid biotas in the north. At such a time, certain northern populations which found themselves in the path of new environmental stresses may have been able to penetrate the southern humid belt by crossing the narrow desert strip in the far north-west. Isolation of this group would have been completed by a southerly swing of the central deserts. A number of oscillations of similar nature would have enabled both *leucoptera* and *pileata* to acquire greater tolerance for aridity and thereby extend their ranges. *Pileata* probably continued to expand eastwards after the Last Glacial cycle until it came into contact with 'chrysoptera.'

Mayr's assertion that intergradation occurs where the ranges of these two subspecies meet is confirmed by three skins in the South Australian Museum from Clare in the south-west interior of New South Wales, and another from Lucindale, South-East of South Australia. All these show the streaked back and "dull black" head of 'chrysoptera,' but are otherwise like *pileata*. A skin from Coleraine, Victoria, shows only the features of *pileata*.

*Neositta* seems to have had a long history in northern Australia during the greater part of the Tertiary and its spread to southern Australia has been due to the climatic changes which commenced towards the close of that
period. From one point of view, the races pileata and leucoperta could be regarded as the end members of a series of intergrading populations encircling Australia, but the true end members of this series seem to be pileata and lathami.

As already mentioned, Serventy has attempted to explain the evolution of the chestnut-shouldered wrens (Malurus elegans, pulcherrimus, lamberti, and amabilis) with reference to refuge areas and Post-Glacial arid cycles. Like Neositta, this group seems to have had a northern origin, whilst the 'typical' blue wrens, cyaneus, melanotus, callainus, and splendens would have arisen in the south. The split between the two groups is an ancient one, as indicated by the wide divergence between individual members of each.

In South-west Australia, elegans, pulcherrimus, and splendens are relict forms, the lastnamed being the western representative of the 'blue and black' wrens of southeastern Australia. The form elegans must have been the first of the chestnut-shouldered group to establish itself in South-west Australia in more pluvial times, and it has continued to prefer humid habitats; its ecological equivalent in eastern Australia is the nominate race of lamberti.

Present distribution shows that pulcherrimus is a declining form which once had a wider range in the western half of southern Australia and that it is rather sensitive to arid cycles. The absence of taxonomic differences in the isolated population on Eyre Peninsula is an indication that pulcherrimus must have been completely differentiated before the close of the Last Glacial interval, when it probably ranged south of a line which could be drawn from about Shark Bay to the western margins of the Lake Eyre region. At this time its habitat would have been within the humid moisture zone and it seems certain that it could not have endured conditions much more arid than at present.

Serventy has submitted some evidence by way of breeding records and skins that pulcherrimus and lamberti may not be conspecific, yet the proper status of the former might still be considered doubtful. Except for the presence of a deep violet-blue tinge on the throat and chest, the male of pulcherrimus cannot be separated from lamberti, and females are indistinguishable. It will be apparent that should hybridisation occur between the two forms, great difficulty could be experienced in distinguishing intergrades, even in skins, when "hybrids" would presumably resemble one or other parent form. Both lamberti and pulcherrimus occupy similar habitats, and breeding records in the same area at the same time do not necessarily mean that no 'hybridisation' occurs. The geographical position of pulcherrimus, and the fact that the presence of a blue throat and chest is shared with elegans seems to indicate that the first-named constitutes some sort of link between the latter and lamberti.

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