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The Nomenclature of Biogeographic Elements in the New Zealand Biota

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Abstract

IN the past, several different systems of names have been used for the elements in the New Zealand biota by botanists, zoologists and paleontologists. In an attempt to provide a single nomenclature of biogeographic elements in both plants and animals, living and fossil, terrestrial and marine, the name Malayo-Pacific is proposed for the elements variously termed Malayan, Malaysian, Palaeotropic or Indo-Pacific and the name Austral for the elements often called Antarctic, Subantarctic or Fuegian. The Austral is divided into two sections of contrasting age and differing history: Neoaustral and Paleoaustral. In addition, Australian, Holarctic, Endemic and Cosmopolitan elements are recognised.

INTRODUCTION

IN Hutton's (1873) early essay on the Geographical Relations of the New Zealand Fauna, published shortly after his magnificent production of catalogues of various animal and fossil groups in the Colonial Museum, he did not classify New Zealand animals into faunal elements, but expressed his views on the successive geological events that led to their immigration and evolution. The events he listed (and some of the organisms attributed to them) were as follows:

(1) Formation of a southern continent in the Lower Cretaceous with connections to South America, Australia and South Africa. At this time, he considered, the fauna gained *Galaxias, Leiopelma, Peripatus, Naultinus,* Ratites, *Notornis,* and probably other peculiar New Zealand birds.

(2) After a period of subsidence in the Eocene, a Melanesian-Polynesian continent extended to Lord Howe Island, New Caledonia, and some distance into Polynesia. To this he attributed the immigration of *Sphenoecus,* rails and bird genera from Australia.

(3) Mid Tertiary subsidence followed, and New Zealand entered an archipelagic phase, during which the moas speciated.

(4) Lower Pliocene elevation linked the islands, but did not join them to other lands.

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(5) Upper Pliocene subsidence led to the present geography.

Despite the many advances in New Zealand biology and geology, some of Hutton's concepts remain valid, for instance those of Cretaceous land extension and austral biotic influence, of later dominance by influences from the tropics, and of archipelagic stages in the history of New Zealand.

Later in his productive life, Hutton (1904) gave a short account of the biogeographic elements of the New Zealand Fauna (see Table I). The main elements were repeated under different names by later writers, but Hutton's Ethiopian, Oriental, and Atlantic Island elements have no equivalents in other classifications.

Cockayne (1919), dealing with the flora, recognised Hutton's four main faunal elements, mostly under different names, his Fuegian covering relationships with Chile and the subantarctic islands (Hutton's Antarctic), his Malayan Element including also plants of Polynesian affinity and presumed origin. His less important European and Cosmopolitan elements correspond, very roughly, with the animals of diverse and distant affinities that Hutton classed in five minor elements. Despite these differences, the correspondence between a botanical and zoological approach is quite marked.

Table I.—NEW ZEALAND BIOTIC ELEMENTS.

Hutton, 1904	Cockayne, 1919	Cockayne, 1921-1928	Oliver, 1925	This Paper
Aboriginal	Endemic	{ Endemic { Palaeozelandic	[Palaeozelandic]	Endemic
Malayan and Melanesian Oriental	Malayan	{ Palaeotropic { Lord Howe-Norfolk	Malayan	Malayo-Pacific
Australian	Australian	Australian	Australian	Australian
Antarctic	Fuegian	Subantarctic	South American [" so-called Antarctic "]	Austral { Neoaustral Austral { Paleoaustral
Palaearctic	European		—	Holarctic
Nearctic Ethiopian Neotropical Atlantic Island	} Cosmopolitan	Cosmopolitan	—	Cosmopolitan

In *The Vegetation of New Zealand* (1921), Cockayne proposed a classification of floral elements (Table I) that has been widely quoted by later writers and was repeated in the second edition of the same work (1928). The Palaeozelandic, proposed for an ancient New Zealand element that "had originated on her own soil", overlaps widely with the Endemic Element, but also includes groups inferred to have spread from New Zealand to other areas, and was stated to be difficult to disentangle from the Subantarctic Element. The name Palaeotropic was used for the element often termed Malayan, indicating inferred derivation from the tropics of the Old World, not necessarily an *old* element from the tropics. A small Lord Howe-Norfolk Element was added. In recent quotations (Millener, 1960; Allan, 1961; Rattenbury, 1962) the Lord Howe-Norfolk Element is omitted.

Oliver (1925) dealt with both fauna and flora in a classic paper. Like Hutton in 1873, he did not classify the biotic elements, but discussed the history of the fauna and flora in geological time, using data from fossils and emphasising the events that influenced dispersal. He used the terms South American, Malayan and Australian elements in his text but referred without approval to Cockayne's

Palaeozelandic (which he considered an element of mixed origin) and to the " so-called " Antarctic Element (also considered to be a mixture of elements and to be of minor importance).

Forster (1961) classified New Zealand animals in three categories—Archaic, Post-Archaic, and Post-European, implying a lack of confidence in our ability to classify in terms of geographic origin, an attitude that is justified with respect to the elements here termed endemic.

In this paper the term " element " is used for the sum total of organisms that came to New Zealand along a given dispersal avenue, but ecological bonds between the different organisms that used the same dispersal avenue are neither implied nor denied. Classification of organisms by dispersal avenue implies their immediate place of origin, but not their ultimate place of origin. A nomenclature for elements in the New Zealand biota does not cover New Zealand elements in other biotas except for providing pigeon-holes for many organisms of which the known distribution provides a presumptive avenue of dispersal but not an unambiguous direction of dispersal.

The need for a nomenclature for elements in the New Zealand biota, which can serve the purpose of zoologists, botanists and paleontologists alike, led the writer, in recent biogeographic papers (1961, 1962), to introduce several new terms for generally recognised categories. The main source areas for the biota, acknowledged by all who have discussed the subject, are the present cold-temperate region (Antarctic, Subantarctic, Fuegian, etc.), the tropics (Malayan, Malaysian, Palaeotropic, Indo-Pacific), and Australia. Other elements are classed in Endemic, Cosmopolitan, and Holarctic (European, Palearctic) categories.

Marine Organisms

Hutton included marine animals in his classification but Oliver passed them over in his biogeographic paper because he considered that their great vagility prevented their use to determine land connections. New Zealand marine organisms show three dominant influences: (1) tropical-subtropical elements from the north, generally classed as Indo-Pacific (strictly Indo-West Pacific), see Marwick, 1925; (2) cold temperate elements of the Southern Ocean, with circumpolar affinities (see Knox, 1960, for examples); (3) Australian elements, other than those which are parts of 1 and 2.

There are also, of course, endemic and more or less cosmopolitan elements in the marine faunas, and it is possible to recognise bipolar or antitropical elements corresponding in a general way to the Holarctic Element (e.g., *Mytilus edulis* and the King Crab *Lithodes*). Thus the main elements fall into the same major categories as the land biota.

Paleontological Evidence

The remains of successive fossil marine faunas and terrestrial floras preserved in New Zealand sedimentary rocks show varying degrees of relationship to those of other lands. The early Paleozoic faunas have rather far-flung, if not cosmopolitan, affinities. In the Lower Devonian, too, the relationships of the Brachiopoda, in particular, mostly seem to lie with distant northern hemisphere countries, but Gill (1952) has emphasized Australian affinities, and a few forms show relationship with South Africa or South America, the first faint indication of a Southern Ocean biota.

In the Lower Permian, marine invertebrates (Fletcher, Hill and Willett, 1952) belong to a cool-water southern "*Cyathaxonia* facies", as do related contemporary faunas in Australia, South Africa and South America. Moreover, the few Lower Permian plants known (McQueen, 1954) are members of the southern temperate flora, although the better known members of that flora (*Glossopteris,* *Gangamopteris*) have not yet been recorded. In the Upper Permian, by contrast, a strong Tethyan affinity is shown by the reef-corals and fusulinid Foraminifera of Northland (Hornibrook, 1951; Leed, 1956).

In the Triassic and Liassic, benthic faunas are sufficiently distinctive (endemic) to have given rise to the concept of a Maorian Province (including New Caledonia) within the Pacific-Arctic Realm that shows some regional differences from the Tethys, but organisms with planktonic dispersal (ammonites in particular, and some Pterioid bivalves) show that the Tethyan influence remained strong. It becomes dominant in the Middle and Upper Jurassic, when immigrants from the Tethyan Realm (belemnites, ammonites, Trigoniidae, Buchiidae, the brachiopod *Kutchithyris*) dominated the fauna (Marwick, 1953).

The oldest Cretaceous fauna known (Aptian), in the Korangan Stage (Taitai Series), includes one notable Australian genus (*Maccoyella*) and others of more widespread, probably Tethyan, affinity. In the Middle Cretaceous, however, there appear a few elements of predominantly southern distribution, such as the lamellibranchs *Iotrigonia* (s. str.) and *Eselaevitrigonia*, along with further Tethyan (or perhaps cosmopolitan) forms. In the Upper Cretaceous, southern elements are stronger, and include ammonites, bivalves (*Lahillea, Pacitrigonia*) and gastropods related to those of South America and Seymour Island and Foraminifera like those of Burwood Bank, Central and South America (Hornibrook, 1953), in addition to Australian elements such as the Dimitobelidae (belemnites). The Cretaceous vegetation includes many southern Podocarps, *Nothofagus*, and Proteaceae (Couper, 1960). In the Cenozoic, faunas and floras show southern, Australian, and Indo-Pacific influences (for the latter, see Marwick, 1925), but the Indo-Pacific influence (successor to the Tethyan of earlier times) is certainly dominant from middle Eocene to Upper Miocene (Fleming, 1962, Fig. 18). In the Pliocene, however, with regional cooling that culminated in the Pleistocene, the Indo-Pacific influence dies down, and southern and Australian influences are important among the newcomers to the fauna (Fleming, 1952).

As a broad generalisation, therefore, the three major elements used in classifying the geographic affinities of the living fauna and flora can be distinguished in their fossil history. The southern influence was apparently dominant in the Early Permian, the Upper Cretaceous, and the Plio-Pleistocene, and the Tethyan, Indo-Pacific or "tropical" influence in the Upper Permian, middle and later Jurassic, and middle Tertiary. The Australian influence, one suspects, was always present, but is perhaps not always recognised, as Australia also shared in the other two elements (southern and tropical), so that immediate and ultimate origins are hard to disentangle. At no time since the Jurassic can we affirm that any one element was completely lacking among the invaders that characterised successive periods.

Terminology

The names used by successive reviewers for the same elements have varied (Table I). Classification of biotic elements is an exercise in generalisation. The broader a generalisation, the more worth-while it is in summarising experience. The claim is sometimes made that land plants, land animals of different groups, and marine organisms are so distinct in ecology and vagility that they are subject to different rules and cannot be integrated into a single biogeographic scheme. Granted the many differences in colonising ability, however, the dispersal avenues defined by physical factors (currents of air and water, bathymetry, shore-lines, and climatic zones) tend to be shared by different organisms of contrasting habits but of similar geographic origin, especially in a country like New Zealand, where any likely Tertiary land connections have been "isthmian links" flanked by sea, and where marine and terrestrial climates are closely related. Thus the attempt is here made to draw up a single set of terms for New Zealand biotic elements applicable to both plants and animals, marine, terrestrial, fresh-water (Table I, right hand column).

The terms Cosmopolitan, Endemic, and Australian have appeared in previous classifications and need no explanation. The Holarctic is a minor element, of uncertain status, discussed below.

The northern, ex-tropical, element in the New Zealand biota has been recognised as of importance by all writers under the names Malayan and Melanesian, Malaysian, Palaeotropic and Indo-Pacific. The latter (or the more precise term Indo-West Pacific) is in almost universal use among marine zoologists throughout the world. " Malaysian ", with broader implications than Malayan, has been used by overseas writers (e.g., Burbidge, 1960). New Zealand botanists have extended the term Malayan to include plants of inferred Pacific (Melanesian-Polynesian) origin, and few zoologists would claim direct Indian Ocean derivation for Indo-Pacific organisms in New Zealand. The term *Malayo-Pacific* has been coined to cover the New Zealand biotic element of apparent tropical derivation (Fleming, 1962).

The term Austral is here used for what has previously been called the Antarctic, Fuegian, South American or Subantarctic element in the New Zealand biota. The word Austral is used in its primary sense of southern (from the Latin for the south wind) and thus has no particular reference to Australia. It has already been used overseas in the same sense (e.g., by Fosberg, 1948). Skottsberg (1953) used the term with a more restricted meaning for that part of the southern element that " requires a milder climate than the Subantarctic ". More recently, Kuschel (in press*) has suggested that the name Austral be used for a southern biogeographic region characterised by the same biotic elements as are here grouped as Austral. The term "Antarctic " is rejected because it infers that Antarctica necessarily played a part in the history and dispersal of the entire element. " Subantarctic " has restrictive ecological and climatic implications, inappropriate to many members of the Austral Element (e.g., podocarps). " Fuegian " and " South American " both have an undesirable bias towards one sector in the broad circumpolar field implied by the concept. Two subdivisions of the Austral (Neoaustral and Paleoaustral) have been proposed elsewhere (Fleming, 1961, 1962) and are discussed below.

DISCUSSION

The three dominant elements in the New Zealand biota correspond with dispersal avenues that are still to some extent open, and with mechanisms that are still operating. Ex-tropical storms and the southern distributaries of the South Equatorial Current still bring Malayo-Pacific birds and marine organisms and floating candel-nuts and coconuts to our coasts. The northern subtropical influence, chiefly from the Malayan and Melanesian areas, was apparently stronger at times in the past when the Trade-Wind belt expanded southward or when the submarine ridges running northward from New Zealand were more emergent than they now are.

The Austral element includes plants and animals distributed by the West Wind Drift of air and water-masses and its contribution to the biota has apparently been greatest when climatic zones moved northward (in the Pliocene and Pleistocene) and also, perhaps, as many have suggested, following Hooker (1847), when a temperate and vegetated Antarctica provided a route broken by narrower sea barriers than in post-Pliocene time.

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There is, indeed, a strong contrast in degree of endemism, in dispersal ability, and (on the whole) in age of dispersal between the extremes among the Austral elements, as pointed out by Dawson (1958). The younger group includes species of plants and animals that have either not differentiated into geographic races since they became widely distributed in a circumpolar subantarctic zone "as if showing that distribution is now actually taking place" (Oliver, 1925), or have merely sub-speciated to form easily recognisable representative forms. Some members of this group have colonised islands that were severely glaciated during the Pleistocene. Their post-glacial dispersal has certainly been across the sea, and some of them have obvious adaptions for such dispersal. Moreover, their fossil record in New Zealand (if any) is generally short, seldom extending back beyond the Pliocene, suggesting that some of them first came to this country as climatic zones moved north during the period of late Tertiary cooling or during the Pleistocene climatic fluctuations that followed. I have elsewhere named this element, apparently distributed for the most part under present geographic and climatic conditions, the *Neoaustral* (Fleming, 1962). It includes seaweeds, such land plants as *Acaena adscendens, Ranunculus biternatus, Sophora* (*Edwardsia*), subantarctic grasses; several mollusca including *Mytilus edulis, Aulacomya, Argobuccinum; Larus dominicanus* and other seabirds; earthworms (*Microscolex*; Lee, 1959) and perhaps some insect groups. It corresponds to the austral part of Forster's Post-Archaic category (1961). The implied direction of Neoaustral dispersal is eastward, down the West Wind Drift, but the sector of origin is seldom obvious. Oliver (1924) pointed out that large plant genera in any one of the continental regions commonly have one or two outliers or even a regular trail to the eastward, and Fell (1962) has shown how echinoderm genera from each southern land area have apparently spread down-wind leaving a diminishing trail of species.

The contrasting older Austral element, distinguished as *Paleoaustral** (Fleming, 1961) consists of representative species of genera, or endemic genera of southern families, which have not re-colonised formerly glaciated islands in post-glacial time, and which seem poorly adapted for trans-oceanic dispersal. In fact, the degree of endemism of the separated members suggests that they have been thoroughly isolated for a considerable time since their parent stocks were separated, and their fossil record in New Zealand and elsewhere confirms their ancient (Tertiary or Mesozoic) dispersal. The Paleoaustral element includes the Podocarps, *Nothofagus,* Proteaceae, *Fuchsia, Laurelia,* etc.; the Struthiolariidae among mollusca; and many terrestrial invertebrates that have been cited as evidence for Antarctic land connections. Doubtless transoceanic dispersal contributed to the Palaeoaustral element. *Fuchsia,* for instance, must have reached Tahiti across the sea and could therefore have reached New Zealand without land connections.

Some Paleoaustral plant genera, usually listed as of Antarctic origin (e.g., Skottsberg, 1953, p. 95) are first recorded as fossils in New Zealand during the Eocene-Miocene interval when the dominant biotic influences were Malayo-Pacific (Fleming, 1962). Such for instance are *Laurelia, Coriaria, Griselinia, Astelia* and *Aristotelia.* It has been speculated that some of these may have originally been Malayo-Pacific elements that entered the Austral region during the Tertiary (Fleming, 1962, p. 104) and subsequently spread eastwards, like the echinoderms discussed by Fell (1962). Oliver (1925, p. 134) long ago suggested that this was the case for *Coriaria* and *Aristotelia.* The distribution of *Fuchsia* suggests the opposite direction of movement but too little is known of

* The term Antarcto-tertiary (as used, for instance by Axelrod, 1959) is not synonymous with Paleoaustral, though it overlaps.

Tertiary floras in the Atlantic-Indian sectors of the Southern Ocean to refute an eastward dispersal in this case too. The directions and means of dispersal of the Paleoaustral elements are in fact unknown; the biogeographic term Paleoaustral is intended merely to embody the conclusion that there was once a circumpolar dispersal avenue more efficient than the present one that gave rise to the Neoaustral element.

The distinction between Neoaustral and Paleoaustral elements is here considered to be important in southern hemisphere biogeography. On the one hand, those who believe that some Paleoaustral elements (e.g., podocarps, *Nothofagus*) were distributed by land connections do scant justice to their case by including Neoaustral elements (such as *Azorella*) as part of the problem to be solved. On the other hand, those who suspect that such southern elements as *Nothofagus* and Podocarps could have been dispersed across the sea are guilty of wishful thinking if they maintain that these Paleoaustral elements could have been as easily distributed by the same dispersal mechanisms (the same quantitatively as well as qualitatively) as have evidently distributed the Neoaustral elements. Whereas the Neoaustral Element is apparently still being distributed, the Paleoaustral evidently ceased its dispersal long ago. The only reasonably certain conclusion is that the Paleoaustral element found circumpolar dispersal easier at some times in the past than it is now—at least by reduction in the width of ocean barriers when Antarctica was free of ice and vegetated, if not by extensions of land, or by pre-Tertiary approximation of land-masses prior to continental drifting. Paleontological evidence indicates that Paleoaustral immigration to New Zealand was spread over a considerable interval of Mesozoic and Tertiary time.

Australia, the nearest land-mass to New Zealand, with its distinctive biota, is well placed to supply New Zealand with colonists that used the prevailing westerly winds and the powerful Tasman Current, but the trans-Tasman route is unlikely to have been made easier in the past by shallows or island stepping stones. Many northern and southern elements are shared by Australia and New Zealand, and could have come to New Zealand via Australia or directly from the north or south. The biogeographer can therefore be reasonably sure he is dealing with an Australian element only if it is not known from other regions.

Overlap between the different elements is inevitable. Even the Austral element probably consists largely of organisms derived from the north by one or other of the three projecting land areas, as Oliver (1952) concluded for plants and as Fell (1962) has demonstrated for some echinoderms, and as must apply to all organisms for which an ultimate northern or tropical origin is inferred. Organisms that are at the same time Neoaustral and bipolar present a special problem.

Most classifications have included a Cosmopolitan Element for those embarrassing organisms so widely distributed that they cannot be attributed to any of the three main dispersal avenues used by the elements discussed above. Refined systematic studies (or merely circumstantial evidence) sometimes point to the immediate source of New Zealand stocks of a cosmopolitan species. The biogeographer can minimise the Cosmopolitan Element by determining the routes by which some of its members entered the New Zealand area and can redistribute them among other elements, but he cannot dispense with it in his classification.

The Endemic Element also presents a challenge to biogeographers. Most endemic species and many endemic genera show relationships overseas by which they can be allocated to one of the other elements. Many endemic genera of New Zealand birds, for instance, are demonstrably of Australian derivation (Falla, 1953). But endemic families and higher categories can seldom be attributed unambiguously to one particular source area. This applies, for instance, to the Onycophora and other terrestrial invertebrates, to the moas and kiwis among birds, to the Tuatara among reptiles, and the bat *Mystacina*—they may have originally been Australian, or Malayo-Pacific, or even (conceivably) Austral elements. Forster (1961) has recently used the term "Archaic" for such organisms, but they vary greatly in age. Within an endemic element, it is always important to distinguish the primary endemics (due to local evolution) from the secondary (or relict) endemics due to extinction elsewhere of formerly widespread groups. In New Zealand the Apterygiiformes are evidently a primary endemic group, the Sphenodontidae a secondary endemic.

Cockayne's name Palaeozelandic was proposed for a special segment of the endemic element, for "genera now more or less widespread", of Tertiary New Zealand origin, "which had originated on her own soil". It thus refers not to the secondary or relict endemic elements but to the primary endemic element and to groups of New Zealand origin that have spread to other regions. Oliver (1925, p. 122) commented that the Palaeozelandic Element is of mixed origin, and later discoveries, particularly of fossils, have shown that some of its members are Austral rather than "Zelandic" and thus secondary endemics, but the concept of New Zealand as a site of Mesozoic and Tertiary evolution of groups that have spread to other regions remains a valid one (e.g., for the species of *Hebe* in Chile). The "Palaeozelandic" is, however, a category more useful to biogeographers of recipient countries than to the New Zealander.

Hutton listed Palearctic and Nearctic elements in New Zealand, but most of his examples would now be classified under different headings. The following species of land and fresh-water birds belong to groups that are otherwise almost entirely north temperate: the New Zealand Scaup (*Aythya novaeseelandiae*), the Auckland Island Merganser (*Mergus australis*, formerly also on the mainland), the South Island Pied Oystercatcher (*Haematopus ostralegus finschi*), and the Black-billed Gull (*Larus bulleri*, a member of the *ridibundus* group). Moreover, it is at least a plausible hypothesis to suppose that the endemic Charadriiformes (species of *Charadrius, Pluvialis*, and the endemic genus *Anarhynchus*) may have arisen as resident populations from Holarctic migrant ancestors. There are also many plants (*Euphrasia* according to Du Rietz, 1948) and invertebrates that form similar disjunct outliers of Holarctic groups. To be sure, such elements may have formerly been cosmopolitan and have come by either Australian or Malayo-Pacific dispersal avenues to New Zealand before their extinction over vast intervening areas on their presumed routes. But in the absence of definite evidence that such organisms were once Australian or Malayo-Pacific, a Holarctic element has been allowed in the classification. Marine organisms that are bipolar or antitropical in temperate or sub-polar latitudes (e.g., *Catharacta skua* and *Fulmarus* among birds; *Mytilus edulis* and the King Crab *Lithodes* among invertebrates) also present classificatory problems but have not here been given the status of a separate element. The examples cited are Neoaustral elements in the New Zealand fauna, distributed in the west wind drift, and their broader antitropical distribution is a matter of global, rather than local biogeography.

Such difficulties in classifying minor elements do not detract from the importance of the three chief dispersal avenues—Malayo-Pacific, Austral and Australian —that evidently contributed the main elements of the New Zealand biota. The names here proposed for these elements are submitted for scrutiny by specialist workers in botany and zoology in the hope that a single terminology may lead to greater intergration and clarification of biogeographic concepts and to a greater liaison between the separate disciplines in this field.

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