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BIODIVERSITY RESEARCH

Research on New Caledonian terrestrial fauna: achievements and prospects

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Abstract. This paper summarizes what is known about the New Caledonian terrestrial fauna and discusses opinions on its nature and origins. An overview of relations with neighbouring areas points out links with New Zealand and southern faunas for many ancient or non-mobile indicators, whereas many recent, or mobile indicators, give evidence of Australian or Oriental influences through the Inner Melanesian Arc. It seems that the uniqueness of the fauna, and its old original basis, have been frequently underestimated. Studies on fossil vertebrates give evidence of recent extinctions, and bird surveys indicate that this process is still continuing. It is assumed that information acquired through biodiversity studies will facilitate the enforcement of a better conservation policy in New Caledonia.

Key words. Terrestrial fauna, New Caledonia, origins, dispersal, faunistic links, extinction, conservation.

INTRODUCTION

Research on the New Caledonian fauna began soon after the island came under French rule (in 1853). After a decade of pioneers came twenty-five years of intense scientific activity (1860–84). During this period, much work was carried out by church ministers and sailors; then interest seems to have languished until the Sarasin & Roux expedition (1911–12) which gave rise to a brilliant revival. They published the famous serial *Nova Caledonia*, the zoological parts of which were printed between 1913 and 1926. After World War II scientific expeditions conducted by the Osaka Museum, the University of Vienna, the Bishop Museum and by many American, Australian and New Zealand Institutions have all contributed significantly to the advance of our faunistic knowledge. The presence of an ORSTOM Research Centre in New Caledonia since 1947 had also made the work of both French and foreign scientists easier. This activity has been recently increased by coordinated research on biodiversity and by cooperation between scientists of many laboratories and nations working in the same field (Tillier, 1988; Chazeau & Tillier, 1991).

THE STATE OF WHAT WE KNOW

Table 1 summarizes the numbers of species in the various classes and orders that have been recorded from New Caledonia and the Loyalties, totalling less than 4500 species. When compared with the number of recorded phanerogams (3250), it clearly indicates an incomplete inventory. A five- to fifteen-fold increase may well be expected but three phyla are lacking, or have not yet been recorded, and many major groups are absent.

Chiroptera are the most interesting mammals, with endemic *Pteropus*, *Miniopterus* and *Notopteris* (Sanborn & Nicholson, 1950; Felten, 1964). The discovery of new taxa can still be expected in the microchiroptera living in caves. Birds are well known and much more diverse, with one monogeneric family (Rhynochetidae), three genera and sixteen species endemic to the mainland or the Loyalties. Major revisions have been achieved on reptiles but further studies of their distribution may reveal some new taxa (see pp. 107–122, this volume). Geckos and skinks are of the greatest interest, with eight endemic genera, radiation being observed in four. Terrestrial snakes and amphibians seem represented by only introduced species (Sadlier, 1986; Bauer & Vindum, 1990). Most freshwater fishes originate from brackish water. Therefore, the idea of a depauperate fauna is generally accepted, notwithstanding the existence of a puzzling endemic galaxiid, *Nesogalaxias neocaledonicus*

(Weber & de Beaufort), 1913.

Important fossil sites have been discovered since 1974. Valuable data have been acquired on Pleistocene vertebrates (Poplin, 1980; Balouet & Buffeteau,

Table 1. New Caledonian metazoa.

Phylum		Subphylum		Class		Subclass		Order	
Sponges	5								
Platyhelminthes	39			Turbellaria	22				
				Trematoda	1				
				Cestoda	16				
Nemathelminthes	2			Nematoda	2				
Annelida	44			Oligochaeta	41				
				Achaeta	1				
				Hirudinea	2				
Mollusca	213			Gastropoda	210	Prosobranchia	30		
						Pulmonata	*c.* 180		
				Bivalvia	3				
Arthropoda	4018	Chelicerata	318	Arachnida	318			Scorpiones	4
								Pseudoscorpiones	6
								Amblypygi	1
								Opiliones	3
								Aranea	185
								Acarina	119
		Antennata	3700	Crustacea	100	Branchiopoda	7		
						Copepoda	11		
						Malacostracea	82	Isopoda	50
								Amphipoda	2
								Decapoda	30
				Myriapoda	88	Diplopoda	50		
						Chilopoda	38		
				Entognatha	51			Collembola	45
								Diplura	6
				Insecta	3461	Apterygota	6	Archaeognatha	3
								Thysanura	3
						Pterygota	3455	Ephemeroptera	13
								Odonata	42
								Blattodea	37
								Isoptera	10
								Mantodea	3
								Dermaptera	18
								Orthoptera	125
								Phasmatodea	30
								Embioptera	3
								Psocoptera	43
								Phtiraptera	30
								Hemiptera	*c.* 350
								Thysanoptera	31
								Neuroptera	14
								Coleoptera	*c.* 1500
								Siphonaptera	3
								Diptera	410
								Trichoptera	19
								Lepidoptera	524
								Hymenoptera	*c.* 250
Vertebrata	157			Pisces	33				
				Amphibia	1			Anura	1
				Reptilia	44			Squamata	44
				Aves	68				
				Mammalia	11			Rodents	4
								Chiroptera	7

1987; Balouet & Olson, 1989), but fossils are still lacking for most groups. The bird fauna was much more diversified than today, with eleven species of non-passerine birds now extinct. They included a giant *Sylviornis*, a megapod and a second species of rhynochetid bird. All lived in the dry forests along the west coast, as did many extinct passerines which have not yet been studied. Though fossil reptiles remain poorly known, conspicuous members of the extinct fauna have been identified: a giant horned turtle, a primitive terrestrial crocodile and a monitor lizard. Pleistocene fossils also include the same species as today. Fossil mammals other than bats, rats and humans are obviously lacking.

What we know about invertebrates varies greatly, both from a quantitative and a qualitative standpoint. Not much is known of freshwater sponges nor of most groups of 'worms', among which Annelida are best inventoried. The land snails fauna is amazingly rich and diverse, with high levels of endemism (Solem, 1961, 1964; Solem, Tillier & Mordan, 1984). New Caledonia has a small but interesting fauna of scorpionids, pseudoscorpionids and opilionids. Spiders are much more diverse (Raven & Churchill, 1988, 1990; Raven, 1991). Acarina have been extensively collected, but most familes need serious study.

Entognathes display a rich and diverse fauna of Collembola, with much endemism at generic and specific levels (Deharveng & Najt, 1988; Weiner & Najt, 1991). Some major books and papers have been published recently on the orders Diptera (Evenhuis, 1989), Lepidoptera (Rhopalocera & Macroheterocera: Holloway, 1979; see also this volume), Psocoptera (Smithers & Thornton, 1974; Thornton & Smithers, 1974), Odonata (Lieftinck, 1975), Ephemeroptera (Peters, Peters & Edmunds, 1978; Peters & Peters, 1980), Trichoptera (Ross, 1975) and Dermaptera (Brindle, 1976). A number of specialized papers deal with families, tribes or genera in Orthoptera (Gryllidae), Coleoptera (Cerambycidae, Chrysomelidae, Scydmaenidae, Elateridae, Coccinellidae, Scarabaeoidea) and Diptera (Tabanidae, Bombyliidae, Dolichopodidae, Muscidae, Drosophilidae, Ceratopogonidae, Mycetophiloidea), but important gaps still exist in Microlepidoptera, Hemiptera (especially Heteroptera), Hymenoptera and in most families of Coleoptera and Diptera.

Endemism in insects is high at the species and generic levels, particularly in the less mobile groups (100% in Psocoptera, Ephemeroptera, some Coleopterous families like Pselaphids; 80% in Blattodea; 70% in Phasmatodea and Dermaptera; even 38% in the much more vagile Lepidoptera). Radiation is important in many genera.

THE NATURE AND ORIGINS OF NEW CALEDONIAN FAUNA

Divergent opionions have been expressed on the origins of the New Caledonian fauna and on the relative importance of vicariance and dispersal patterns.

In his classic book on island biology, Carlquist (1974) favours dispersal. He estimates that New Caledonia, with no mammals and no adaptive radiation in birds, is essentially oceanic. He recognizes patterns of adaptive radiation in reptiles but states that relict taxa are few among the insects. To explain the rich fauna of land snails, he suggests a colonization by a more vagile founder, gigantism in *Placostylus* being part of an adaptive radiation program. Diamond (1984) states that 'from its vertebrate fauna, one could not have guessed that New Caledonia even existed before the Pleistocene'. He classifies New Caledonia as 'continental' for lizards, but not for birds. He also favours a general pattern of recent arrivals, not one implicating a Gondwanan origin for the fauna.

Other contributions on this matter originate from Bishop Museum entomologists, who studied the mechanism of transoceanic dispersal in the Pacific and provided valuable zoogeographic information through an extensive review of published data. Gressitt (1961) observes indications of considerable age in faunal patterns and points out that the New Caledonian fauna holds a position by itself, and is not easy to classify as oceanic (for the lack of mammals other than bats and rats and the disharmony in insect fauna) or subcontinental (because the fauna is fairly rich, with many endemic genera).

Many scientists will probably agree with Bauer (1989); further discussions of continental and vicariant patterns of any group versus oceanic and dispersive patterns should integrate vagility (including behaviour), antiquity and phylogenetic relationships with neighbouring faunas. Some bias should be avoided: birds and mammals do not constitute the bulk of the fauna in any area; generalizing properties of dispersability as displayed by some members of a group, to the group itself, can be misleading; the nomenclatural basis used should reflect phylogeny; fossils should be included in discussions based on fragile vertebrate faunas.

RELATIONSHIPS WITH NEIGHBOURING AREAS

Vicariant and dispersal patterns can be found when one considers different groups, but also within the same group.

What we know today of a much more diversified Pleistocene fauna should modify our views on birds. Radiation has existed in many genera (*Accipiter*, *Porphyrio*, *Tyto*, Rhynochetos). *Megapodius*, *Sylviornis*, *Porphyrio* and *Rhynochetos* seem dubious candidates for overseas colonization. Rhynochetos are related to the New Zealand *Aptornis*, with hypothetical South American affinities. This fauna has been noticeably modified by migrants, because New Caledonia has always been within the range of dispersal of many birds. These colonizing birds seem to have originated from multiple neighbouring areas (Berlioz, 1945, 1962; Diamond, 1984).

A few migrant reptiles are Pacific wides, but similarities between New Caledonia and other island groups are very low at the species level. The fauna remains highly original at the generic level, which indicates very long island isolation (Bauer, 1989). Recent fossil reptiles also increase significantly the 'continental' aspect of New Caledonian vertebrates. But a Gondwanan origin for the galaxiid fish seems inconsistent with drastic changes in freshwater biota through the Eocene. It has been suggested that a marine ancestor may have dispersed from Australia during the Pliocene and then become restricted to the lakes in Southern New Caledonia (MacDowall, 1968).

Patterns in the invertebrates are not easy to synthesize. Solem (1958) estimates that New Caledonia and Vanuatu had separate connections with New Guinea, leading to great differences in land snail faunas, but charopid and rhytidid land snails belong to Gondwanan groups.

Diplopod relationships are oriental. The buthid scorpio *Isometrus (Reddyanus) heimi* Vachon, 1976 belongs to a Gondwanan group and may indicate vicariance; two *Hormurus* are endemic or Melanesian. Relationships in pseudoscorpionids are Melanesian or Micronesian. Anapid spiders are endemic at the species and generic level, but they belong to a group of Australian and New Zealand genera (Platnick & Forster, 1989). Relationships in the argyopid *Archemorus* are with Australia and New Guinea. In Collembola, affinities are Gonwanan: Australian and subantarctic for *Dinaphorura* (Tullbergiinae) (Najt, 1988); South African for *Caledonura* and *Parectonura* (Neanurinae) vicariants of *Australonura* from Australia and New Guinea (Deharveng, 1988). *Blattodea* have 80% endemic species; all the apterous or subapterous species have strong Australian affinities (*Polyzosteria*, *Platyzosteria*, *Stylopyga*), but no recent work has reviewed generic classification. Almost all Psocoptera are endemic. Thysanoptera display great Australian influence. In Phasmatodea, the high endemicity in Eurycanthinae suggests isolation and great age; non-endemics are strictly Melanesian with one New Zealand species. A similar pattern exists in Dermaptera. Gressitt (1971) noted that cerambycids and chrysomelids suggest that New Caledonia is much older than neighbouring islands and has preserved old elements, some of which have evolved locally under long isolation.

The pattern is quite different in more mobile Odonata. They have no endemic families or subfamilies nor any true paleogenic element of the Australian continent. Even the autochthonous elements are of comparatively recent northern and western polyphyletic origin. Their general distribution has been compared with that of birds and is in agreement with the idea of drastic Eocene changes in freshwater biotas (Lieftinck, 1975). Other freshwater insects, such as Ephemeroptera or Trichoptera, display characters related to genera in New Zealand, Australia and Tasmania; but no attempt has been made to clarify the phylogeny (Ross, 1975; Peters & Peters, 1980). Micropterigids, eriocranids and hepialids are obviously archaic Lepidoptera, but affinities in most Lepidoptera familes are complex, with possibly ancient patterns in groups of oriental affinities, penetration by Australian genera and also modern patterns. This is explained by a complex series of dispersal (Holloway, 1984; see also this volume).

Roughly summarized, many ancient or non-mobile indicators show links with New Zealand and Southern faunas, and also with Australia; many recent or mobile ones indicate Australian influences or oriental influences through the Inner Melanesian Arc.

To explain faunal affinities, sea mounts are now widely accepted as an alternative to the hypothesis of vanishing land masses. Recent research in the south western Pacific reveals numbers of such sea mounts, especially along the Lord Howe and Norfolk Ridges: variation of sea level could have generated much more emerging land than was previously assumed. This strengthens the theory of stepping stones, favouring dispersal long after the complete isolation of the Norfolk Ridge and of New Caledonia at the end of Lower Cretaceous; there is some evidence of such flux in the Lower Miocene. Alternatively, such a series of islands could have been adequate for speciation through isolation, or for conservation of old faunal elements, with the eventuality of these faunas gathering later on remaining lands.

THE UNIQUENESS OF THE NEW CALEDONIAN FAUNA

As pointed out by Gressitt (1967, 1971), the New Caledonian fauna is unique in many groups. This uniqueness may be attributed to the extinction of faunas in neighbouring areas and to a long evolution of surviving groups after partial subsidence.

We may still be able to retain the relatively high percentage of endemic birds and the peculiarity of many present forms, which can be related to the stabilization of archaic elements, notwithstanding the high ecological pressures from recent colonizers. What we know today about the recently extinct fauna gives strength to this opinion. We may also retain the great species and generic diversity in gekkos and skinks which are primarily endemic. Many invertebrate groups also display unusual diversity: richest area for Philotarsid Psocoptera, richest Pacific Island group for Phasmatodea, richest area for micropterigid Lepidoptera (Gibbs, 1983). Evidence of high originality is found in molluscs, Collembola and in most groups of insects lacking vagility (Blattodea, Dermaptera, some Coleoptera).

Archaism is observed in many non-vagile groups such as Phasmatodea (*Asprenas*, *Clitarchus*). This pattern has been strengthened by recent research, for instance, the discovery of Archostemmata (Cupedidae) (Nebois, 1984) or the description of Podoscirtine gryllids *Adenopterus* and *Archenopterus* (Otte, Alexander & Cade, 1987). Archaism is also observed in more mobile groups such as micropterigids (Zeugloptera), and we know that members of the primitive family Agathiphagidae (Aglossata) exist in New Caledonia, though none have yet been described.

The geographical position of New Caledonia may explain the general pattern of the fauna: the ante-Eocene stock has radiated through long isolation, and has then been modified by mobile colonizing taxa dispersing from different origins at different times. It is perhaps surprising that this old original basis for the fauna has been so frequently underestimated, although well recognized in the flora. The uniqueness of the fauna was probably masked by a focus on conspicuous mobile groups or by lack of modern taxonomic revisions. It seems, however, that zoologists can now agree with Thorne (1963): 'New Caledonia, because of its highly endemic, distinctive biota, is a subregion rather than merely a division in the Oriental Region'.

PRESENT THREATS TO THE FAUNA

Fossil birds indicate recent major extinctions correlated with the arrival of humans and rats. *Sylviornis* were abundant in sites dated 1700 years BP, and there is some evidence that they were hunted by humans, along with *Porphyrio* and may be *Mekosuchus* (Balouet, 1987). The extinction of the great Kagu *Rhynochetos orarius* Balouet & Olson, 1989, which lived in the sclerophyllous forest of the west coast and could not adapt to the rain forest – as did *R. jubatus* Verreaux & des Murs, 1860 – is a striking case caused by drastic environment alteration.

The process is still continuing. Noticeable extinctions in the last century include the New Caledonian Wood Rail, the New Caledonian Lorikeet and the Giant Skink. These species are known only by the type and by rare and questionable reports of visual contact. The endemic Painted Button-quail, formerly widespread on the west coast and in Pine Island, has not been captured for the last fifty years and is, at least, relictual in dry forest patches near Nepoui. The Ouvea Crested Parakeet is still an endangered species. The emblematic Kagu was selected in 1982 as a world priority in bird protection: populations do not exceed a few hundred individuals, with evidence of recent extinctions.

One can easily imagine that many other more discrete species went the same way. What is involved is progressive anthropization, with an increasing predatory pressure in shrinking biota. An immediate answer will be to enforce a strict conservation policy for the most fragile vegetation associations, in order to establish a new equilibrium between humans and nature in New Caledonia. Scientists concerned with nature conservation should play an active role, by organizing biodiversity studies in such a way that they help authorities to stay on the tight track. Recent work illustrates how much can be discovered through coordinated research on New Caledonia biota.

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