

## NEW ZEALAND'S GENETIC DIVERSITY

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**ABSTRACT:** The known genetic diversity represented by the New Zealand biota is reviewed and summarised, largely based on a recently published New Zealand inventory of biodiversity. All kingdoms and eukaryote phyla are covered, updated to reflect the latest phylogenetic view of Eukaryota. The total known biota comprises a nominal 57 406 species (c. 48 640 described). Subtraction of the 4889 naturalised-alien species gives a biota of 52 517 native species. A minimum (the status of a number of the unnamed species is uncertain) of 27 380 (52%) of these species are endemic (cf. 26% for Fungi, 38% for all marine species, 46% for marine Animalia, 68% for all Animalia, 78% for vascular plants and 91% for terrestrial Animalia). In passing, examples are given both of the roles of the major taxa in providing ecosystem services and of the use of genetic resources in the New Zealand economy.

*Key words:* Animalia, Chromista, freshwater, Fungi, genetic diversity, marine, New Zealand, Prokaryota, Protozoa, terrestrial.

### INTRODUCTION

The original brief for this chapter was to review New Zealand's genetic resources. The OECD definition of genetic resources is 'genetic material of plants, animals or micro-organisms of value as a resource for future generations of humanity' (UN 1997). This is derived from Article 2 of the 1992 Convention on Biological Diversity (CBD), which defines genetic resources as 'genetic material of actual or potential value', and Article 1 of the Andean Decision 391 defines 'genetic resources' broadly as 'all biological material that contains genetic information of value or of real or potential value' (WIPO 2010). The term 'resources' is conceptually linked to the notion of benefit to humanity (Frankel and Soulé 1992, p. 241), and since the CBD is also concerned with access and benefit-sharing, the precise meaning of 'genetic resources' has been subject to discussion and debate in the light of new technologies, new scientific knowledge and bioeconomic developments (e.g. genomics, proteomics and synthetic biology) (Schei and Tvedt 2010).

Allem (2000) argued that, since keystone species carry ecological value that could affect economic activity, they should be upgraded to become a genetic resource. Allem also noted how, in the language of the CBD and derivative documents, genetic resources were taken to be a subset of 'biological resources'; Article 2 states "*Biological resources*" includes genetic resources, organisms or parts thereof, populations, or any other biotic component of ecosystems with actual or potential use or value for humanity.' He pointed out that the two terms had, even by 2000, overlapped considerably in use and application and argued that they should be treated synonymously, and, since 'genetic resources' has been a long-established term (since the early 1960s), the principle of priority should be observed, with 'biological resources' being redundant in this context.

The semantic looseness of terminology used in the otherwise legal context of the CBD (a continuing problem acknowledged by Schei and Tvedt (2010)) moved Allem to argue for precision: 'For instance, while flying over a humid forest it seems normal to refer to biological resources lying down there. But this is a manner of speaking. In other words, in order to know what lies down there, one must get closer and then either genetic resources or biodiversity will emerge from the previous anonymity ... Wild cassava and wild potatoes remain biological diversity until man finds some economic or scientific use for them. Then, they become a genetic resource ... A resource is 'something to which one can turn for help or support or to achieve one's purpose' (Oxford Dictionary)' (Allem 2000).

Article 10b of the CBD calls for signatories to 'Adopt measures relating to the use of biological resources [i.e. genetic resources] to avoid or minimize adverse impacts on biological diversity [e.g. genetic diversity]' (my parentheses). An inventory or stocktaking of indigenous genetic diversity can aid the identification of potential genetic resources, guided to a considerable extent by previous discovery, identification, and utilisation of such resources. Accordingly, since the focus of this volume is the services provided by indigenous and man-modified (e.g. agricultural) ecosystems in New Zealand, this chapter reviews what is known of New Zealand's *total* indigenous and naturalised-alien genetic *diversity*, which includes, in the language of the CBD, 'genetic material of actual or potential value'. This diversity excludes domesticated, zoo and aquarium animals (unless feral) and the many thousands of horticultural species, varieties and cultivars, which are dealt with in other chapters.

Pre-European Māori were the first to scope New Zealand's genetic diversity and genetic resources, through collecting and naming, and through trial and error and the passing-on of discoveries and learned knowledge, which continued beyond European introductions of foreign species; for example, they almost certainly developed a range of new potato cultivars, by selection from seedlings and from somatic mutations, of introduced cultivars (Harris 2001, 2005). Formal systematic documentation of New Zealand's flora and fauna, including marine, began with Cook's first voyage in 1769. Cook's second voyage (1773–74), and those of Louis Duperry and Dumont D'Urville in 1824, 1827 and 1840, also yielded a useful quantity of specimens and data for overseas scientific study. With the founding of several scientific societies, provincial museums, and university colleges during the second half of the 19th century, a remarkably advanced infrastructure for the indigenous documentation of the biota was established, with a mostly amateur scientific base. The first major floras published by indigenes, based on their own and previous work, appeared around and just after the turn of the century (Kirk 1899; Cheeseman 1906) and Hutton (1904) published a complete index of the known fauna. In the spirit of these works from a century earlier, and arising out of CBD-related imperatives like the New Zealand Biodiversity Strategy and the Species 2000/ITIS Catalogue of Life, a project was launched in early 2000 to review and inventory New Zealand's total Phanerozoic biodiversity (Gordon 2002). Involving 238 taxonomic experts in 19 countries, the project was completed in 2012 with the publication of the third of a trilogy of volumes (Gordon 2009, 2010, 2012a). The comprehensive data in the chapters, checklists and tables

in these volumes, as well as in papers published subsequently, are the main source of information for this chapter. A report on New Zealand's biological resources prepared for the former Ministry of Economic Development that was based on data used for the biodiversity trilogy (Sim-Smith et al. 2005) has also been consulted.

### THE GEOGRAPHIC BASIS FOR NEW ZEALAND'S GENETIC DIVERSITY

New Zealand is a geographically isolated archipelago comprising two major islands and more than 700 offshore islands and islets. Its western coast is 1600–2250 kilometres from Australia; it has a land and freshwater area of 268 680 square kilometres (larger than the United Kingdom), and an Exclusive Economic Zone (EEZ) of almost 4.2 million square kilometres that spans 30 degrees of latitude and exceeds 15 times the land area. Collectively, the mainland and smaller islands of New Zealand are the visible surface of a large submerged continental mass that extends beyond the boundaries of the EEZ. This landmass, geologically known as Zealandia, extends from New Caledonia's Chesterfield Plateau (about 19° S) in the north-west and the Colville and Kermadec ridges in the north-east to south of New Zealand's subantarctic islands at about 56° S. The combined seafloor area of the plateaus and ridges is about 6 million square kilometres; the emergent land is only about 7% of the area of continental crust represented by Zealandia (Campbell et al. 2008). The New Zealand region comprises a Large Marine Ecosystem (LME no. 46 out of 64 globally). The same area also more or less corresponds to the World Wildlife Fund so-called Global 200 New Zealand Marine Ecoregion.

New Zealand owes the large size of its EEZ, possibly the fifth-largest in the world after those of the United States, Australia, Russian Federation, and French Polynesia, to the widely distributed emergent outer islands of Zealandia. Hence, subtropical Raoul Island, at 29°15' S on the Kermadec Ridge, is about 1000 kilometres from the North Island coast, the Chatham Islands are 800 kilometres east of South Island, and the farthest subantarctic island – Campbell Island – is 640 kilometres south of South Island at 52°30' S. The legal concept of an 'extended continental shelf' encompasses the whole area underlain by continental crust and includes the shelf and slope. Hence, New Zealand's extended continental shelf is potentially 1.7 million square kilometres (Gordon et al. 2010).

The latitudinal spread of New Zealand, coupled with the varied seafloor relief, is accordingly mirrored by the wide diversity of marine habitats. Half the area of the existing EEZ is shallower than 2000 metres but the seafloor dives to hadal depths in the Puysegur and Kermadec trenches, the latter to just over 10 000 metres. The New Zealand coastline is very long; estimates range from 15 000 to 18 000 kilometres, the exact length being confounded by its fractal quality, influencing maritime and littoral genetic diversity. On land, the geology, soils and landscapes are equally varied, reflected in the various terrestrial and freshwater ecosystems and species associated with them, whether through elevation (alpine to lowland) or rock or sedimentary type (e.g. volcanic, karstic, ultramafic). Among others, the late Oligocene inundation of the New Zealand landmass and Quaternary glaciation, volcanism and uplift of the Southern Alps profoundly influenced the evolution of our biota in the Neogene (Graham 2008). Anthropogenic modification of the New Zealand landscape and coast, accompanied by the introduction of thousands of alien species, many of which have become naturalised, has been

the most recent factor shaping New Zealand's genetic diversity.

### PROKARYOTES

#### Overview

Globally, there are about 11 400 accepted species of prokaryotes (Euzéby 2013). In New Zealand, there were 671 named bacterial species (Table 1) as of the end of 2011. This figure includes cyanobacteria ('blue-green algae'), archaeobacteria (archaea) and all other bacteria (eubacteria) (Young et al. 2012; Broady and Merican 2012; and additional archaeobacteria references in the present chapter). The New Zealand checklist of cultured bacteria published by Young et al. (2012) includes only those species for which there is at least one reference strain held in a public culture collection. Although additional bacterial species have been recorded as present in New Zealand, the accuracy of earlier reports is uncertain. Environmental genetic screening has determined a much greater level of prokaryotic diversity than is evidenced in the formal list of published names. This is because studies have not yet been made of the many bacteria that can be isolated from particular environmental sites. Estimates are that 1–10% of the major bacterial groups have been cultivated and characterised and there exist major groups for which no members have been cultured. At present it is not clear why the 'yet to be cultivated' (YBC) bacteria cannot be grown in pure culture. Explanations involve interdependencies of bacteria in communities and the role of organic and inorganic surfaces as necessary for bacterial activity. However, it has not been demonstrated that these bacteria differ in any fundamental way from bacteria already characterised. For example, where significant effort is made to understand the specific requirements of bacteria, as in anaerobic rumen or dental-plaque research, as many as half of the bacteria have already been cultured. It may be that more sophisticated incubation conditions involving attention to available nutrients, oxygen regulation, acidity, toxicity, and temperature will produce conditions suitable for other YBC bacteria.

Molecular evidence suggests that free-living species have a global distribution. For example, though there may be internal diversity within species, strains of *Pseudomonas fluorescens* or *Bacillus thuringiensis* from North America or Australasia do not appear to be readily distinguishable from those from Europe, sharing identical protein structures and having no unique elements (Sim-Smith et al. 2005). Genetic diversity may have arisen within species, but the selective effects of local environments have maintained essentially the same species phenotype in the common micro-environment found around the globe. It is a matter of conjecture whether endemic bacteria (other than cyanobacteria) exist in New Zealand. One would need to demonstrate not only the presence of novel taxa here but also their absence elsewhere. However, ecological niches where endemic taxa may be anticipated would include isolated extreme environments (e.g. geothermal areas) or where co-evolution occurs with endemic eukaryotes. An example of the latter concerns nitrogen-fixing bacterial symbionts (*Rhizobium*) in native legumes and non-rhizobial bacteria of the genus *Frankia* in *Coriaria* and *Discaria*. Nominally endemic eubacteria and an archaeobacterium have been isolated from geothermal environments (e.g. Niederberger et al. 2006). Because they have enzymes that can function at high temperatures, research has been carried out to exploit such prokaryotes for commercial processes (such as providing enzymes to be added to detergents that maintain their activity at high temperatures and pH). Archaeobacteria are often mutualists or commensals. One example is the methanogens that inhabit

TABLE 1 Species diversity of the New Zealand biota (figures slightly modified from Gordon 2009, 2010, 2012a)

Taxon (kingdom/ phylum)	Described	Known undescr./ undet.	Estimated undisc.	Terrestrial	Marine	Freshwater	Endemic	Adventive
BACTERIA	671	30	Unknown	306	82	358	Unknown	Unknown
Archaeobacteria	5	0*	Unknown	0	2	3**	5	Unknown
Cyanobacteria	372	30	>200	15	40	352	19	1
All other bacteria	294	0*	Unknown	291	40	3**	Unknown	Unknown
PROTOZOA	507	32	570–770	331	53	198	24	23
Euglenozoa	108	7	>100	6	17	96	8	1
Percolozoa	7	6	8	2	0	5	1	0
Loukozoa	16	3	65	16	0	3	6	9
Amoebozoa	338	11	350–550	306	3	80	6	13
Sulcozoa	1	0	3	0	1	0	1	0
Choanozoa	37	5	45	1	22	20	2	0
CHROMISTA	4039	169	4595–4695	490	2540	1286	283	287
Ochromytha	1765	30	1260	16	858	939	55	14
Pseudofungi	151	10	9	136	4	23	1	106
Bigyra	14	1	35	1	9	6	0	3
Miozoa	384	57	1370	148	249	49	32	115
Ciliophora	340	7	1100	149	78	175	50	37
Cercozoa	80	4	135	38	20	53	10	9
Retaria	1182	35	405–505	0	1217	0	128	3
Cryptista	17	0	30	0	10	7	1	0
Haptophyta	82	13	210	0	93	2	3	0
Heliozoa	24	12	40	2	2	32	3	0
PLANTAE	7440	115	1075–1175	5770	702	1091	2395	2585
Glaucophyta	1	0	1	0	0	1	0	0
Rhodophyta	473	89	35	0	541	20	189	15
Chlorophyta	566	19	610	35	156	394	29	10
Charophyta	527	7	65	1	0	533	43	1
Bryophyta	1124	0	62	1088	0	35	396	36
Tracheophyta	4749	0	300–400	4646	5	108	1738	2523
FUNGI	8045	350	23 525	8213	89	191	1663	1993
Incertae sedis	3	0	0	3	0	0	0	0
Chytridiomycota <sup>Δ</sup>	150	1	175	106	6	39	7	13
Microsporidia	12	6	9000	12	3	3	5	6
Zygomycota	89	0	170	72	0	17	10	19
Glomeromycota	38	1	5	39	0	0	0	2
Ascomycota	5238	79	9065	5210	77	128	780	1485
Basidiomycota	2525	263	5110	2771	3	4	861	481
ANIMALIA [Table 2]	27 946	8071	35 340	19 629	14 500	2163	22 991– 23 005	2247
TOTALS	48 640	8766	65 100– 65 500 <sup>◊</sup>	34 739	17 966	5287	27 380– 27 394	4889

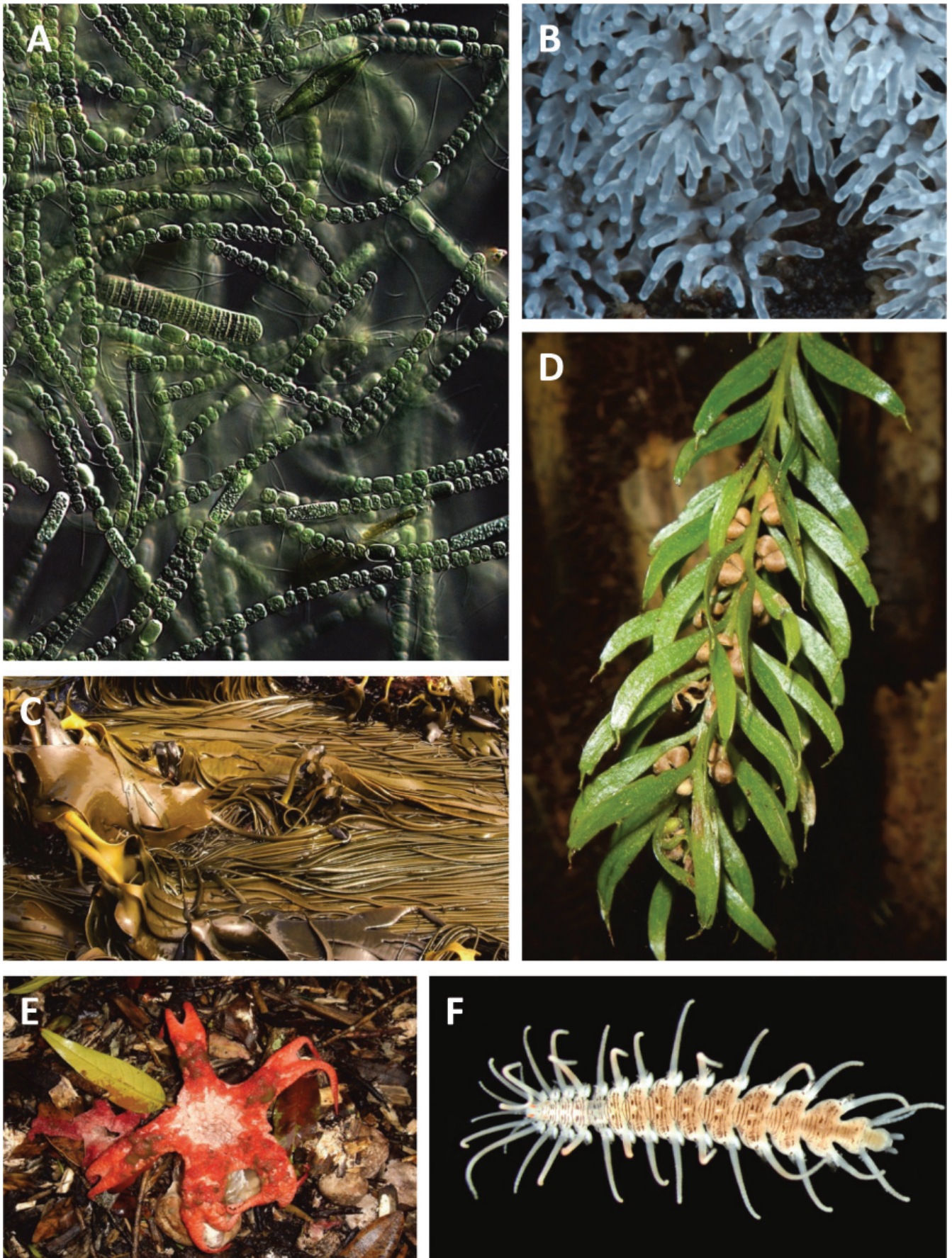
\* None reported in culture in Young *et al.* (2012)

\*\* geothermal

<sup>Δ</sup> *sensu lato*

<sup>◊</sup> Eukaryota only

Note that for major-habitat tallies (terrestrial, marine, freshwater) some species occur in more than one column



**FIGURE 1** Exemplars of the six kingdoms of life in New Zealand. A, Bacteria: filaments of *Anabaena inaequalis* (Cyanobacteria). B, Protozoa: fruiting bodies of slime mould *Ceratiomyxa fruticulosa* (Amoebozoa). C, Chromista: bull kelp *Durvillaea antarctica* (Ochrophyta). D, Plantae: psilopsid *Tmesipteris sigmatifolia* (Tracheophyta). E, Fungi: octopus stinkhorn *Clathrus archeri* (Basidiomycota). F, Animalia: polychaete *Amblyosyllis granosa* (Annelida). Photos: A, Faradina Merican. B, Clive Shirley. C-E, Dennis Gordon. F, Geoff Read.

the gut of humans and ruminants, where their vast numbers aid digestion. Thus, from a New Zealand perspective, archaeobacteria are the cornerstone of the agricultural economy. Methanogens are used in biogas production and sewage treatment and the methane they produce is a major greenhouse gas. Overseas, archaeobacteria have been enlisted to aid in cleaning up petroleum spills, but a number of eubacterial taxa, including *Acidovorax*, *Burkholderia*, *Mycobacterium*, *Nocardia*, *Pseudomonas*, *Rhodococcus*, *Sphingomonas*, and *Terrabacter*, also have biodegradative properties, and are potentially useful in bioremediation. Studies have been conducted on New Zealand species of several of these genera (e.g. Aislabie et al. 1997).

The pathogenic bacteria of humans and domestic animals have a worldwide distribution and were most likely all introduced. But there are likely indigenous pathogens that evolved in association with native vertebrates. For example, *Mycobacterium pinnipedii*, a member of the *M. tuberculosis* complex, appears to be adapted to fur seals in the southern ocean (Hunter et al. 1998) but on occasions it can affect cattle. Plant-pathogenic bacteria in New Zealand are mostly associated with introduced horticultural crops, the latest pathogen of economic concern being an introduced virulent strain of *Pseudomonas syringae* pathovar *actinidiae* (Psa-V) on kiwifruit. Less often native plants are affected, such as the phytoplasma *Candidatus Phytoplasma australiense*, a pathogen also found in Australia, which has been linked to dieback of the cabbage tree *Cordyline australis*, some other native plant taxa, and the strawberry. Overall, there is a paucity of pathogenic bacteria on native plants, which appear to be less susceptible than domesticated cultivars. Relatively few bacterial genera are pathogens of insects in New Zealand. *Bacillus thuringiensis* is the best-known insect pathogen worldwide and is the basis of a large biopesticide industry. It is a common soil and plant-surface inhabitant in New Zealand but has rarely been recorded as causing disease in nature. However, imported commercial preparations of *B. thuringiensis* have been vital in pest-control efforts where use of chemical pesticides was not an option. In 1998, huge amounts of *B. thuringiensis* serotype *kurstaki* were applied over urban Auckland to eradicate an introduced pest, the spotted tussock moth, in one of the heaviest aerial applications of this bacterium in the history of its use. This subspecies is also a vital component in New Zealand's organic kiwifruit-production systems (Young et al. 2012).

Gut-biome bacterial diversity is a fruitful area of research. Abundant studies have been made on humans and ruminant animals and, increasingly, studies are being applied to rarer animals from a conservation perspective since gut-associated microbes are important in nutrition and pathogen defence. For example, a study of the microbiome of the critically endangered New Zealand parrot, the kākāpō *Strigops habroptilus*, has revealed low phylum-level diversity, consisting almost exclusively of Firmicutes and Gammaproteobacteria (Waite et al. 2012). This study provides a baseline for further microbiological study of this species.

Cyanobacteria have been recorded from New Zealand's terrestrial environments but these have not been comprehensively sampled and only 15 species are known to date. Worldwide, several hundred species have been recorded from soils. Flint (1968) did some pioneering work; subsequent studies by Everitt (1998) and Novis (2001) revealed a significant flora in soils from lowland to high-alpine regions. Five new alpine species and a new genus, *Godleya*, were recently described just from Arthur's Pass National Park (Novis and Visnovsky 2011). Prominent growths

of cyanobacteria encrust rock in moist mountainous regions, the supralittoral of rocky shorelines, and dim-light and artificially lit zones of limestone caves, but much taxonomic work has to be done. On the other hand, a species found among the wool fibres of dead sheep was determined to be *Gloeocapsa sanguinea* (Cassie Cooper 1996). Other taxa (particularly species of *Nostoc*) occur in symbiotic associations with native *Gunnera*, possibly 8% of our lichen flora, some thallose liverworts, and all hornworts. Broady and Merican (2012) have reviewed all these occurrences and highlighted human uses of cyanobacterial diversity overseas that could be applied in New Zealand.

#### *Prokaryotes in fresh water*

Globally, and in New Zealand, the environmental sampling of microbial species richness in natural aquatic environments is at a relatively early stage and knowledge of aquatic genetic diversity of bacteria (other than pathogens and cyanobacteria) is much less than for terrestrial diversity. Eubacterial populations in fresh unpolluted water have mostly arisen from activity in terrestrial environments and transportation into streams and lakes, or they are intimately associated with organic material in water (Sim-Smith et al. 2005). Bacterial communities are considered responsive indicators of changing environmental conditions and offer significant advantages as bioindicators of environmental health. Several recent studies have been undertaken on bacterial communities of biofilms in New Zealand streams, with applications to assessing ecological health in stream restoration (e.g. Lear et al. 2008, 2009, 2012).

Freshwater cyanobacteria in New Zealand are represented by 352 described species and range from microscopic unicells to large, colonial alga-like masses (Broady and Merican 2012). Relatively few (c. 19 species) are endemic, including one from peat-bog pools. More species are found in the North Island than the South. They are a common component of periphyton (encrusting/film communities) in standing and flowing waters but study of periphyton in lakes lags behind that of phytoplankton and periphyton of flowing waters. Some cyanobacteria are periodically problematic in shallow eutrophic lakes; at least eight cause blooms and several of these are potentially toxic, especially *Anabaena flos-aquae*, *A. spiroides*, *Microcystis aeruginosa* and (restricted to South Island brackish Lakes Ellesmere (Waihora) and Forsyth (Wairewa)) *Nodularia spumigena*. Warm dry summers can cause nuisance proliferations of mat-forming taxa (e.g. species of *Oscillatoria*), some toxic enough to kill dogs. These occurrences and the roles of cyanobacteria in freshwater plankton and periphyton have been summarised by Broady and Merican (2012).

New Zealand's hot springs and other geothermal waters harbour extremophiles, including thermophiles, acidophiles, and thermoacidophiles (Mountain 2012). The upper limit for cyanobacteria is about 70°C. Only non-photosynthetic bacteria can survive in hotter water; species of *Thermus* tolerate more than 70°C in New Zealand and hyperthermophilic *Sulfolobus acidocaldarius* lives at more than 80°C. Patel et al. (1986) isolated several species of anaerobic sulphur-metabolising archaeobacteria (including *Thermoproteus* and *Desulfurococcus*) from New Zealand hot springs with temperatures above 85°C.

#### *Prokaryotes in the marine environment*

From its sea shores to its ocean trenches, New Zealand has a wealth of varied habitats and potential biological hosts but taxonomic sampling of prokaryotes throughout the marine

environment is in its early days. As biomass, the most abundant form of life is bacteria in ocean sediments, simply because the seafloor is the largest realm on the planet, and the commonest constituents of oceanic plankton, supplying a significant fraction of Earth's atmospheric oxygen, are cyanobacteria. Archaeobacteria are also abundant. Marine bacteria are assumed to be cosmopolitan; the same species have been reported from seas in the Northern and Southern hemispheres, although there may be locally adapted groups associated with coastal organisms. Bacteria are present in relatively high concentrations in coastal and estuarine waters.

Marine bacteria are halophilic, requiring high salt concentrations for growth, or halotolerant, capable of growing in a range of salt concentrations. There have been few studies of marine bacteria in the New Zealand EEZ. Isolations from inshore and coastal environments, largely from sediments, are halophilic genera – *Aquimarina*, *Cellulophaga*, *Cobetia*, *Exiguobacterium*, *Flectobacillus*, *Glaciecola*, *Leeuwenhoekella*, *Listonella*, *Marinomonas*, *Microbacterium*, *Microbulbifer*, *Planomicrobium*, *Pseudoalteromonas*, *Psychrobacter*, *Roseobacter*, *Stappia*, *Sulfitobacter*, *Tenacibaculum*, *Vibrio*, *Zobellia* – and halotolerant genera also associated with terrestrial environments, namely *Aneurinibacillus*, *Arthrobacter*, *Bacillus*, *Curtobacterium*, *Flavobacterium*, *Halomonas*, *Isopericcola*, *Kitasatospora*, *Micrococcus*, *Paenibacillus*, *Planococcus*, *Pseudomonas*, *Roseobacter*, *Rhodobacter*, *Rhodococcus*, *Sanguibacter*, *Stenotrophomonas* and *Streptomyces*. Not all these genera have been identified to species. Other unidentified marine isolates represent hitherto uncharacterised genera (Young et al. 2012).

Crenarchaeote archaeobacteria are represented exclusively by hyperthermophiles, most of which either reduce sulphur under anaerobic conditions or oxidise it if they can grow aerobically. The majority of crenarchaeote isolates have been obtained from submarine hydrothermal vents, frequently 'black smokers', which occur at tectonic plate boundaries. Studies in which habitats have been screened using molecular probes for YBC isolates indicate that more than 30% of the total microbial biomass of all marine environments is archaeobacterial and from currently uncultivated organisms (DeLong et al. 1999). Black smokers occur at some vent sites along the Kermadec Ridge, and bacterial mats, frequently of sulphate-reducing *Beggiatoa*, are a common feature at a number of the vent environments on Kermadec seamounts. Unidentified archaeobacterial methanogens and eubacterial *Beggiatoa* and *Thiothrix* are associated with cold seeps at several locations off the New Zealand coast (Sommer et al. 2010). The extent of microbial diversity from seeps along the Hikurangi Margin is currently being studied at the Max Planck Institute for Marine Microbiology, Bremen. Four euryarchaeote taxa, two of them marine, have been formally described from New Zealand, all species of *Thermococcus* (Ronimus et al. 1997; Miroshnichenko et al. 1998; González et al. 1999).

Several types of marine animals restricted to these vent and seep areas in New Zealand obligately harbour bacteria that provide their primary or sole source of nutrition (thiotroph and methanotroph). These include siboglinid polychaetes (genus *Lamellibrachia*) and bivalves (genera *Bathymodiolus*, *Calyptogena*, *Gigantidas*) (Thurber et al. 2010). A number of marine bacteria are endosymbionts of marine invertebrate taxa that typically feed heterotrophically on planktonic food sources, apparently obligately as they have not been able to be cultured, although it appears that some sponge endosymbionts are neither species- nor habitat-restricted (Taylor et al. 2013). Screening of marine organisms for bioactive compounds has been carried out

for some years, especially on sponges, cnidarians, bryozoans and ascidians, with sponges yielding the most novel marine natural products to date (also true of sponges worldwide), in which microbes can comprise as much as 40% of sponge volume (Taylor et al. 2007), like New Zealand *Ancorina alata* (Kamke et al. 2010). Bacterial community profiles of low-microbial-abundance (LMA) sponges are clearly different from profiles of high-microbial-abundance (HMA) sponges and, remarkably, each LMA sponge seems to harbour its own unique bacterial community. In New Zealand, Chloroflexi are associated with HMA sponges (Schmitt et al. 2012), whereas Alphaproteobacteria dominate in the LMA sponges sampled (Giles et al. 2012). Endemic *Stelletta maori* uniquely harbours only Fusobacteria (Schmitt et al. 2011). A possible new genus of the cyanobacterial order Chroococcales has been found in a native species of *Mycale* (Webb and Maas 2002). In several instances (not yet determined for all source species), the organism synthesising the substance of interest in these invertebrate hosts is an endosymbiont. For example, in Californian populations of the common marine-fouling bryozoan *Bugula neritina* the gamma proteobacterium *Candidatus Endobugula sertula* is the source of the bryostatins that have been tested in human clinical trials for the treatment of various types of cancer (Haygood and Davidson 1997). Two closely related alpha-proteobacterial symbionts – *Candidatus Endowatersipora rubus* and *Candidatus Endowatersipora palomitas* – occur in Californian populations of the bryozoans *Watersipora arcuata* and *W. subtorquata*, respectively (Anderson and Haygood 2007). All three bryozoans are naturalised-alien species in New Zealand; the presence of the bacterial endosymbionts in New Zealand populations has not yet been tested but is highly likely.

## PROTOZOA

Protozoa is a paraphyletic kingdom that includes the ancestors of all other eukaryote kingdoms (Cavalier-Smith 1998, 2010a, 2013). It includes the most basal eukaryote phylum Euglenozoa, the excavate phyla Loukozoa (including Metamonada) and Percolozoa, and the sarcomastigote phyla Amoebozoa, Sulcozoa (including Apusozoa) and Choanozoa. Other major groups formerly generally referred to as protozoans (e.g. foraminifera, radiolaria, ciliates, sporozoans) are now classified among Chromista. Only 507 described and 32 known-undescribed species of Protozoa are known from New Zealand (Gordon 2012a), with the greatest recorded diversity in terrestrial settings (Table 1).

### *Terrestrial diversity*

Some 328 species are known from the New Zealand terrestrial environment, mostly soil testate amoebas and slime moulds and parasites of terrestrial hosts. Testate amoebas are a polyphyletic group that includes lobose and filose forms. All have a tectum or test but the filose forms have a different ancestry from the lobose and are included in the chromist phylum Cercozoa. Soil testates are abundant in New Zealand but many regions are incompletely sampled and numerous new taxa are likely to be found. Sampled beech-forest litter was found to contain 542–9392 individuals in a millilitre of soil water (Stout 1963). Protozoan populations are dependent on an adequate bacterial population. Mixed and disturbed soils contain modified, generally much-reduced, testate numbers and diversity. To date, 85 named species of Arcellinida (Amoebozoa) and 32 of Euglyphida (Cercozoa) have been found in New Zealand, only 20–30% of the total number expected in a country of comparable area (Meisterfeld et al. 2012), attributed

to undersampling. Many are cosmopolitan or Gondwanan; some are more restricted. Only a few taxa are endemic or apparently so.

Formerly classified as fungi, slime moulds in the broad sense comprise four groups. 'Acrasiomycota' (acrasid slime moulds) are now classified as Percolozoa, 'Plasmodiophoromycota' (plasmodiophorids) are Cercozoa, and the balance (cellular slime moulds or Dictyosteliomycota and plasmodial slime moulds or Myxomycota) are Amoebozoa. Amoebozoan slime moulds are phagotrophic bacterivores and can be abundant in some habitats, especially temperate forests with much plant detritus. They have a naked amoeboid stage in their life cycle. There are 234 named species in three classes in New Zealand (Meisterfeld et al. 2012). Like soil testate amoebas, New Zealand's slime-mould assemblages are generally compositionally similar to those found in many other parts of the world and show minimal endemism. Nevertheless, the dictyosteleid fauna is distinctive, with three endemic species.

The euglenozoan class Kinetoplastea includes two semi-cosmopolitan bodonids, *Bodo saltans* and *Neobodo designis*, which have been found in terrestrial and aquatic environments, and introduced *Trypanosoma lewisi*, a parasite of Norway and ship rats. Class Euglenoidea includes three euglenoids of damp terrestrial settings (Allison and Broady 2012). Phylum Percolozoa, with only seven species in New Zealand, includes two widely distributed acrasid slime moulds, *Acrasis rosea* and *Pocheina rosea* (Charleston and Stephenson 2012).

Phylum Loukozoa, now including the anaerobic Metamonada as a subphylum (Cavalier-Smith 2013), comprises a small fauna of 19 native and introduced (with hosts) parasites and gut-commensals (Charleston et al. 2012), 16 of them land-based. Some are found in native termites; bacteria associated with the protozoans digest wood cellulose ingested by the termite, liberating sugars that are used by the bacteria, protozoans and host. Trichomonads include several introduced species that infect vertebrates including humans. The best-known of these are *Tritrichomonas foetus* (found in cattle and cats), *Trichomonas gallinae* (mostly in pigeons), *Trichomonas vaginalis* (infecting the human urogenital system) and *Histomonas meleagridis* (the causative agent of 'blackhead' in galliform birds). Two named trichomonad species respectively infect the endemic gecko *Woodworthia* 'Southern Alps' and a termite. Introduced *Giardia duodenalis* (class Trepomonadea) is the cause of giardiasis, a notifiable disease in New Zealand since 1 July 1996. The potential for genetic research on Metamonada in New Zealand is high, both on taxa that infect humans and economically important vertebrates and on the endosymbiotic fauna associated with native arthropods and other animals.

The only terrestrial species of Choanozoa found in New Zealand is the semi-cosmopolitan amoeboid species *Nuclearia simplex*, found in moist soils (as well as fresh water) (Gordon 2012c).

#### *Protozoans in fresh water*

There are 120 taxa (96 species and 24 subspecific taxa) of Euglenozoa in New Zealand fresh waters (Allison and Broady 2012). All but four species are euglenoids, the balance comprising bodonids – ubiquitous creatures of bacteria-rich habitats, one of which (unnamed) is a novel form from a geothermal pool near Matamata (von der Heyden et al. 2004). The euglenoids are mostly grass-green (sometimes orange-red) autotrophs but a small number are colourless chemoheterotrophs. In New Zealand, euglenoids tend to be common in habitats rich in decaying organic

matter, including sewage-treatment ponds, where they are a prominent component of the phytoplankton. The photosynthetic species help oxygenate the water whereas chemoheterotrophic feeding has a role in the mineralisation of organic wastes. Farm ponds, temporary puddles, and ditches contaminated by livestock are likewise well-known sources of euglenoids. One species, *Euglena mutabilis*, is characteristic of acidic waters, including not only geothermal waters but also acidic streams draining coal-mining areas, where it seems to be a useful indicator.

The genus *Naegleria* is the best-known representative of phylum Percolozoa in New Zealand (Charleston and Stephenson 2012), mainly because of the pathogenicity of *N. fowleri*, which can cause fatal primary amoebic meningoencephalitis (PAM) (Cursons et al. 1978). An amoeboid phase lives in soil, feeding on bacteria, yeasts, and organic debris. Food limitation induces a flagellate phase that is able to disperse to more favourable locations. Pathogenic amoebae tend to be associated with warm water having a high coliform content. If a swimmer inhales the flagellate phase it can cross the mucous lining of the nasal cavity and invade the brain, causing haemorrhage, inflammation, and necrosis. Death of the individual can occur within 10–14 days of exposure. It is uncertain how many species of *Naegleria* occur in New Zealand, but there are at least five described species and perhaps four other undetermined species (contaminants of damp contact-lens storage cases) (Gray et al. 1995). Species of congeneric *Vahlkampfia* were co-contaminants. Freshwater/wet-soil Amoebozoa mostly comprise a disparate variety of lobose amoeboid forms, mostly testate. Introduced species of *Acanthamoeba* are found in the same habitats, including geothermal, that are occupied by *Naegleria*, even the contact-lens storage cases (Meisterfeld et al. 2012).

Phylum Loukozoa is represented in New Zealand fresh waters by free-living, semi-cosmopolitan *Reclinomonas americana* (Gordon 2012b) and two species of metamonad parasites (*Monocercomonas batrachorum* and *Trichomitus batrachorum*), found in the rectum of the introduced green and golden bell frog *Litoria aurea* (Charleston et al. 2012). Although *Giardia duodenalis*, in the same subphylum, is an intestinal parasite, its cysts in human and animal faeces can contaminate water. Almost half of the known species of phylum Choanozoa in New Zealand are freshwater species. Most are collar flagellates (class Choanoflagellata), which may be solitary or colonial, free-swimming or attached. Class Ichthyosporea includes three genera (*Paramoebidium*, *Enteromyces*, *Taeniella*) that used to be included in the fungal class Trichomycetes. They are fungoid forms, with a tiny filament-like thallus (often in clusters), which live as commensals of aquatic insects and crustaceans. Class Rozellidea (Cavalier-Smith 2013) is another fungoid group, comprising six species of *Rozella* in New Zealand (Gordon 2012c).

#### *Protozoans in the marine environment*

Marine euglenoids are much less diverse than freshwater taxa, with only six species, but they can be locally abundant, forming films or scums on estuarine mudflats, particularly near effluent discharges. A few are components of phytoplankton. Class Kinetoplastea, on the other hand, is represented by several species of fish-parasitic trypanosomes (Allison and Broady 2012) and marine and maritime bodonids. Marine Amoebozoa are scarcely known in New Zealand, though they certainly exist. Importantly, however, one species, *Neoparamoeba pemaquidensis*, causes amoebic gill disease in farmed salmon; it was

responsible for an outbreak in *Oncorhynchus tshawytscha* and other species may be affected (Diggles et al. 2002). Only a single species of phylum Sulcozoa (Cavalier-Smith 2013), *Collodictyon sphaericum*, is so far known in New Zealand (Gordon 2012d) but its precise relationships need determining by gene sequencing. It was found in Wellington Harbour (Norris 1964) but has not been collected since, so remains nominally endemic. In Choanozoa, some 20 species of marine collar flagellates and two species of fungoid Ichthyosporidia are found in our marine environment (Gordon 2012c).

## CHROMISTA

The constitution of kingdom Chromista has changed since it was first proposed, in 1981, as a third botanical kingdom (Cavalier-Smith 1981, 1986, 1998). It was circumscribed primarily on ultrastructural grounds and has strong molecular support. It largely comprised heterokont algae and related fungoid forms. During the 2000s there was an emerging view of six major groups (supergroups) of eukaryotes, not all equal in size but characterised by their major distinctions: Amoebozoa, Opisthokonta, Rhizaria, Excavata, Chromalveolata, Archaeplastida. Opisthokonta comprised mostly animals and fungi and Archaeplastida were equivalent to plants. The rest were protistan, with Amoebozoa, Rhizaria and Excavata essentially protozoal and Chromalveolata comprising alveolates (e.g. dinoflagellates, ciliates, and Apicomplexa) plus heterokonts and relatives (e.g. cryptophytes, haptophytes, and heliozoans) (see Wegener Parfrey et al. 2006; Lane and Archibald 2008). Since 2007 it has been demonstrated that Rhizaria and Chromalveolata are related (see discussion in Gordon 2012e) and the scope of kingdom Chromista has been expanded to include these two supergroups (Cavalier-Smith 2010a).

All 10 chromist phyla are represented in New Zealand. These are largely described as in Gordon (2012a), with the exception that Foraminifera and Radiozoa have been combined as phylum Retaria, and Myxozoa is now Miozoa (see Cavalier-Smith 2013). These changes are reflected in the management classification of the Catalogue of Life (Ruggiero et al. 2013). Collectively, chromists occupy all major environments, comprising 4208 species (4039 described). The bulk of these are marine (2540 species), with 1286 freshwater species and 490 terrestrial (Table 1).

### Algal chromists

These include some of the most important microalgae of marine and fresh waters and macroalgae (seaweeds). They are thoroughly reviewed by Chang and Broady (2012), Chang et al. (2012), Harper et al. (2012), and Rhodes et al. (2012). Brown algae (phylum Ochrophyta, class Phaeophyceae) comprise 148 species in New Zealand. The largest are the giant kelp *Macrocystis pyrifera*, which can form underwater 'forests' and exceed 20 metres in length, and species of bull kelp (*Durvillaea* species). Brown algae play significant roles in nearshore ecosystems, dominating particular habitats in terms of biomass and structuring three-dimensional space of subtidal reefs. Hurd et al. (2004) provided a summary of published data on New Zealand macroalgal ecology and physiology and the uses of seaweeds, including aquaculture and seaweed extracts. Brown algae are used commercially as human food (sea 'vegetables,' dietary supplements, food garnish, salt substitute), stock food for aquacultured paua, seaweed-based fertilisers and a source of the polysaccharide alginate. *Durvillaea* species are considered taonga by Māori for traditional uses.

Twelve alien brown seaweeds are now part of our biota. Most appear to pose little or no risk to native species whereas the Asian kelp *Undaria pinnatifida* is the most serious marine-algal pest to have entered New Zealand. Although it can be harvested for use, its spread as far as The Snares is alarming. It competes with native seaweeds (in some places occupying 70% of canopy cover) but does not play a similar role as a food and habitat source for intertidal and subtidal organisms (R. Suarez, pers. comm.).

Chromist microalgae have major significance in phytoplankton, as food for aquatic organisms and as sources of atmospheric gases. The most speciose are the diatoms, with 1452 named species in New Zealand. Apart from producing oxygen in photosynthesis, diatoms play a major role in the global cycling of carbon and silicon – they are among the most important photosynthetic organisms in the world. In the sea they are the major producers of new phytoplankton biomass, sustained by fluxes of new nitrogen from deeper water through upwelling or wind/tidal mixing. In spring, on New Zealand's north-east coast and over the Subtropical Convergence near the Chatham Rise, diatoms make up the bulk of total carbon biomass (>95%). Some are nuisance species, whether as microalgal blooms in eutrophic lakes, as semi-filamentous blooms like 'didymo' (introduced *Didymosphenia geminata*) in South Island rivers, and as toxic phytoplankton in coastal waters (e.g. species of *Pseudo-nitzschia*).

In New Zealand's coastal waters there are nearly 70 species of microalgae that form coloured blooms, including 'red tides'. Some 42 of them are toxic or potentially so (Chang et al. 2012) and most are chromists. The silicoflagellates *Pseudochattonella verruculosa* and *Vicicitus globosus* have been implicated in respiratory distress or fish kills overseas but only the latter has been linked to such events in New Zealand. Three species of raphidophytes are toxic; *Heterosigma akashiwo* was implicated in the mass mortality of farmed salmon in Stewart Island in the 1980s. Dinoflagellates (phylum Miozoa) attract attention as they comprise the greatest number of harmful taxa (29 toxic species recorded). Depending on the species, harmful algae blooms (HAB) can cause mass mortalities of a range of marine life or find their way from shellfish to humans, causing such illnesses as neurotoxic shellfish poisoning (NSP), paralytic shellfish poisoning (PSP), diarrhetic shellfish poisoning (DSP), and ciguatera seafood poisoning (CSP). Of these, only NSP and PSP have definitely been linked to episodes involving humans in New Zealand even though DSP and CSP toxins have been isolated from shellfish extracts or particular species of dinoflagellates in coastal waters. There are several fish-killing species in New Zealand. Ichthyotoxic events have involved *Gymnodinium aureolum* off Banks Peninsula, *Karenia brevisulcata* in Wellington Harbour, *K. selliformis* in Foveaux Strait and *K. concordia* in Hauraki Gulf. Toxins produced by *Karenia brevisulcata* exhibit high cytotoxicity in a wide range of marine organisms; a bloom in Wellington Harbour in 1998 caused massive kills of not only fish but invertebrates and seaweeds and also induced human respiratory distress (Chang 1999). It appears to be the most toxic dinoflagellate known.

Phylum Cryptista (Cryptophyta) comprises 17 species in New Zealand, 14 of them photosynthetic (Chang and Broady 2012). Their plastids and other internal structures make their unicells more complex than cells in animals and plants. Freshwater forms are found in lakes, often in poorly illuminated deeper parts, and in nutrient-rich temporary pools. Marine species are found in tidal pools, brackish water, the interstitial water of sandy beaches, and in the open ocean where they can periodically dominate



spring plankton blooms. In June 1979, *Hillea marina* was found at densities of 1.8 million cells per litre. Cryptistan species are among the most widely distributed around New Zealand and, on some occasions, can contribute to more than 50% of the total cell carbon biomass in coastal waters in summer. Ingested cryptistan chloroplasts mediate the blooms of the ciliate *Myrionecta rubra*.

Phylum Haptophyta is represented by at least 92 species in New Zealand (Rhodes et al. 2012), all but two of them marine. The phylum name derives from the short haptonema that protrudes anteriorly from the cell and which was once thought to be an extra cilium but it differs in structure. In some species at least, the haptonema appears to aid in feeding, somewhat like a finger. The haptophyte cell surface usually carries finely sculptured organic scales but these are mineralised in coccolithophores as coccoliths (famous for making up the White Cliffs of Dover). These mostly small (typically < 20 micrometres) flagellates are ubiquitous in nearshore and oceanic waters. Most species have non-flagellated life stages. *Phaeocystis*, a common New Zealand genus, is easily identified by the palmelloid stage of the life cycle when the cells are embedded in a gelatinous capsule. Foamy blooms of *Phaeocystis* colonies can be quite extensive; in 1981, an incidence of 'Tasman Bay slime,' which suffocated marine life, was caused by *P. pouchetii*. Another haptophyte, *Prymnesium calathiferum*, was implicated in fish kills in Bream Bay in 1983.

Haptophytes produce large quantities of the atmospheric gas dimethyl sulphide (DMS), which constitutes a small but significant amount of the total sulphur flux of the planet and contributes to acid rain. *Phaeocystis* is particularly significant; as well as producing large amounts of DMS, and with it acrylic acid (a bactericide and algicide), *Phaeocystis* species produce an ultraviolet-B-absorbing compound that may counteract increases in physiological stress on cells because of UV, including decrease in photosynthetic efficiency, cell reproduction, and cell survival. The coccolithophore *Emiliania huxleyi* can form massive blooms, turning thousands of square kilometres of ocean a milky white colour that can be seen from space; if these blooms impinge on shorelines they can make swimming unpleasant. Commercially, certain haptophyte species are used overseas in aquaculture industries where mass production of cultures provides food for bivalve and fish larvae. Haptophytes are also increasingly used as sources of pigments, polysaccharides, vitamins, and fatty acids, and their potential in pharmaceutical industries is promising (Rhodes et al. 2012).

#### 'Fungal' and other non-photosynthetic chromists

Two chromistan phyla, Pseudofungi (Oomycota) and Bigyra, include taxa that used to be allied with fungi. 'Egg fungi' have major ecological and economic significance. They vary from unicellular to species with extensive mycelia and are widespread in aquatic and terrestrial environments as saprobes or parasites, attacking fungi, other oomycetes, plants, fish and occasionally other animals including humans. Downy mildews, white rusts, and damping-off disease are caused by oomycetes. Beever et al. (2012c) list all 161 species of Pseudofungi known in New Zealand and review the group.

Among others, *Phytophthora* includes many pathogens of cultivated and native plants. *Phytophthora cinnamomi*, which may have been introduced by Māori on taro (*Colocasia esculenta*), affects many species and has caused the death of kauri, avocado, *Pinus* and *Camellia*. At least 32 other species (seven of them not named or identified), probably all naturalised, occur in New Zealand. Kauri dieback disease is attributed to *Phytophthora*

taxon 'Agathis' (PTA). Other damaging pathogenic species affect apples, *Pinus radiata* seedlings, strawberries and citrus. *Pythium*, another cosmopolitan oomycete genus in soils and fresh water, causes damping-off diseases of zoospore-infected seedlings and, sometimes, older plants. *Pythium oligandrum* is both a pathogen and a mycoparasite, causing a 'black compost' disease and significantly reducing yields of *Agaricus bisporus*, the commercially cultivated button mushroom. *Peronospora* and *Plasmopara* species (causing downy mildews) and *Albugo* (white rusts) affect a range of cultivated and native plants. *Albugo candida*, the white-rust pathogen of crucifers, also attacks native *Lepidium ruderales* (Cook's scurvy grass) and is likely to be one of the factors leading to the decline of this species in the wild. In the marine environment, a species of *Haliphthoros* causes gill mycosis in larval and juvenile stages of captive (in experimental grow-out facilities) rock lobster (crayfish) *Jasus edwardsii* (Diggles et al. 2002).

The fungoid members of the small phylum Bigyra in New Zealand (Gordon et al. 2012a) comprise two groups of class Labyrinthulea, the labyrinthulids or slime nets and the thraustochytrids, which superficially resemble fungal chytrids. The sole species of labyrinthulid in New Zealand, *Labyrinthula macrocystis*, has been implicated in the wasting disease of the eelgrass *Zostera muelleri* in the Auckland area. Thraustochytrids are common in the neritic and oceanic water column and sediments, including the deep sea, where they play a role as saprobes. In coastal environments they help break down plant leaves such as those of mangroves. Thraustochytrids have demonstrated economic value as sources of biochemicals important to human health and aquaculture (e.g. Raghukumar 2008). Some strains produce high biomass of omega-3 polyunsaturated fatty acids (PUFAs) and docosahexaenoic acid, and are emerging as sources of other PUFAs such as arachidonic acid and oils that can be targeted for specific uses. Thraustochytrids may help to offset the decline in fish oils as sources of PUFAs.

Non-fungoid members of Bigyra in New Zealand include opalinid parasites of introduced Australian frogs, freshwater bisoecids and the curious intestinal parasite *Blastocystis hominis*, one of the few heterokont organisms to infect humans and also found in other animal species. The well-known freshwater organism *Actinophrys sol* has had a checkered history of classification. Once considered a heliozoan, it was transferred to the Bigyra (see Gordon et al. 2012a) but the Actinophryida is now believed to have evolved from a raphidophyte (Ochrophyta) ancestor (Cavalier-Smith and Scoble 2013).

True Heliozoa (sun protists), primarily Centrohelea, are ubiquitous, tiny unicellular organisms whose diversity is poorly known in New Zealand. There are 24 described species (Gordon 2012f) but sequencing of 18S rRNA genes from samples collected at a range of localities in New Zealand (from seaweed, eelgrass, alpine-tarn sediment, lake water, and soil) has determined that there at least a dozen other species (Cavalier-Smith and von der Heyden 2007; Cavalier-Smith and Chao 2012).

The second most speciose chromist phylum in New Zealand (after Ochrophyta) is Retaria (Foraminifera + Radiozoa), with 1322 wholly marine species (23 brackish) (Hayward et al. 2012; Hollis et al. 2012). The phylum is part of the chromist infrakingdom Rhizaria (eukaryote 'supergroup' Rhizaria). The distribution of benthic species of Foraminifera is influenced by salinity (if brackish), wave and current energy, oxygen, substratum and, in deeper water, the characters of bottom water including calcium-carbonate saturation and surface-water phytoplankton productivity (carbon flux). Some 29 species of foraminifera and

all radiolaria are planktonic, with their distribution strongly influenced by water temperature and their abundance by phytoplankton productivity. In the case of planktic foraminifera, species diversity is highest in the subtropical region of New Zealand around the Kermadec Islands, decreasing southwards to the subantarctic region to just 2–3 species. In contrast, about 100 species of radiolarian are known south of the Subtropical Convergence into colder water, making this group potentially much more useful for measuring environmental and oceanographic change. Foraminifera and radiolaria (and other skeletised chromists like diatoms and haptophytes) are so abundant in ocean sediments and in geological strata, and contain particular isotopic signatures, that they have numerous scientific and economic applications (particularly to the petroleum industry), including high-resolution stratigraphic dating and paleoenvironmental studies (interpretation of past ocean circulation and productivity, climates and sea levels).

In the deep sea, an unusual group of giant arenaceous foraminifera known as xenophyophores is found on the surface of soft sediments. They are particularly abundant under areas of high sea-surface productivity. Their structure is basically plasmodial but can be highly organised. The largest species, part of the benthic megafauna (generally more than 5 centimetres in height), can achieve sizes of 25 centimetres. They add three-dimensional structure to an otherwise even seafloor and their presence is positively correlated with the diversity of smaller organisms at the centimetre-scale just around and under the test (Hughes and Gooday 2004). Seven species are found around New Zealand.

Infrakingdom Rhizaria also includes phylum Cercozoa, a morphologically disparate group united by genetic (phylogenomic) and some ultrastructural criteria. Cercozoa means 'tailed animals' and alludes to the locomotory cilium in many of the species. The group encompasses ancestrally biciliate 'zooflagellates', euglyphid and other filose testate amoebae, shelled phaeodarians (which used to be classified as radiolaria), *Gromia*, phytomyxean plant parasites like *Plasmodiophora* and the invertebrate-parasitic Acetosporea. In contrast with the parasitic forms, free-living cercozoan zooflagellates have been very little studied, even though some of them, like the cercozoans, are the most ubiquitous flagellates in soil and important predators of bacteria in virtually all aquatic habitats. The taxa that make up the Cercozoa used to be distributed among several protozoan phyla, and even in the fungi in the case of the plasmodiophoras; some 83 species are so far known in New Zealand, more than half of them found in fresh water (Gordon et al. 2012b) (for updates in classification of the phylum affecting New Zealand taxa, see Cavalier-Smith and Chao (2012) and Cavalier-Smith and Oates (2012)).

Based on species diversity and economic importance, the chief cercozoan groups in New Zealand are the filose testate amoebae, plant-parasitic plasmodiophorids and mollusc-parasitic Haplosporida. Morphologically, cercozoan testate amoebae differ most notably from amoebozoan testates in their pseudopods (filopodia, not lobopodia). Two cercozoan orders are involved, both in different classes – Tectofilosida (class Thecofilosea) and Euglyphida (class Imbricatea). According to phylogenomic data, the ability to build a test emerged at least three times in the evolution of Cercozoa, the third example being the marine genus *Gromia* (class Gromiidea), which forms large (2–5 mm in diameter) plasmodial, multinucleate organic tests. *Gromia* in New Zealand comprises at least two species – the very common *G. ovalis* of intertidal and shallow subtidal biotopes and an undescribed/unidentified species just discovered at depth on the

Chatham Rise. Deep-sea gromiids are of interest for the trails they leave in mud that resemble those made by some small invertebrate animals. Class Thecofilosea also includes the Phaeodaria, a group of plankton Cercozoans previously classified as radiolaria.

In New Zealand, plasmodiophorids (class Phytomyxea) comprise seven genera and nine species of plant, oomycete, and possibly brown-algal endobiotic parasites. The best known of these is *Plasmodiophora brassicae*, which causes club-root of cabbage and other crucifers. Other introduced species attack perennial ryegrass (a significant component of winter pasture that is also useful in erosion control), wheat, potato, and introduced *Veronica*. *Tetramyxa parasitica* is a widespread parasite of marine angiosperms in various parts of the world that in New Zealand infects *Ruppia megacarpa* in South Canterbury.

Haplosporidans (class Acetosporea) are best known in New Zealand for the disease bonamiosis (bonamiasis) in Bluff oyster (*Ostrea chilensis*). The causative organism is *Bonamia exitiosa* (Hine et al. 2001). It induces cytological and physiological changes in the oyster that deplete energy reserves, leading to mortality. A second *Bonamia*-like organism has been detected in the oyster but no work has been carried out on it. Another haplosporidan, representing a new genus and species taxonomically near the base of the Haplosporida, was found once in aquacultured juvenile and adult paua (Reece et al. 2004).

The remaining major chromist groups to be considered here are the non-photosynthetic members of the alveolate phyla Miozoa and Ciliophora. As now circumscribed (Cavalier-Smith 2013), Miozoa has three subphyla – Protalveolata (sole class Colponemea), Myzozoa (classes Myzomonadea, Perkinsea, and five classes of superclass Dinoflagellata) and Apicomplexa (classes Apicomonadea, Coccidea (Conoidasida), Gregarinea, Haematozoa (Aconoidasida)), not all of which are found in New Zealand. Photosynthetic dinoflagellates (class Dinophyceae) have been mentioned earlier in this account. Non-photosynthetic (heterotrophic) members that are found in our biota include marine, free-living *Oxyrrhis marina* (class Oxyrrhea), two species of noctilucids (class Noctiluca) including the bioluminescent sea sparkle *Noctiluca scintillans*, and the marine-crustacean parasites *Thalassomyces fagei* and *T. marsupii* (class Ellobiopsea) (Chang et al. 2012). Class Perkinsea is represented by the clam parasite *Perkinsus olseni*, which affects several species of bivalves including cockle and pipi, causing abscesses.

The all-important Apicomplexa (of which only infraphylum Sporozoa is found in New Zealand) includes significant parasites of humans and animals. There are at least 159 species, 128 of them Coccidea (Chang et al. 2012). *Eimeria* (Eimeriidae) is well represented in native and introduced animals, particularly domesticated ruminants and poultry, but also pigs, rabbits and brushtail possum. *Cryptosporidium* (Cryptosporidiidae) nominally includes *C. parvum* and *C. hominis* in New Zealand but *C. parvum* appears to be a species complex and the precise number of taxa is unknown. Host species are numerous, including rodents, ruminants, pigs, cats and dogs, passerine birds and poultry, brushtail possum, and humans. *Cryptosporidium* infections are often the cause of diarrhoea in very young domesticated animals, commonly in association with other infections. Compared with other developed countries, the incidence of cryptosporidiosis in humans in New Zealand is relatively high. As elsewhere, cases have been traced to contact with farm animals or contaminated drinking water; both species infect humans but *C. hominis* is more common in urban areas. *Toxoplasma gondii* (Sarcocystidae) is a remarkable parasite that is common throughout the world

and is capable of affecting virtually all mammal species, though the definitive host is the cat (*Felis* spp.), domestic and feral. In New Zealand, infection has so far been recorded in humans and 11 domesticated and wild mammalian and five bird species. *Toxoplasma* is an important parasite of sheep, commonly causing abortion, stillbirths, and perinatal death of lambs. Goats may be similarly affected. Chang et al. (2012) review the other major Apicomplexa in New Zealand, including the blood-parasitic Haemogregarinidae, Haemosporida (including *Plasmodium* spp.) and Piroplasmida of vertebrates and eugregarines of invertebrates.

Phylum Ciliophora (ciliates) comprises about 347 known species in New Zealand but the fauna has been relatively little studied and more than 1000 additional species are likely to be discovered (Foissner et al. 2012). More freshwater species (175) are known than terrestrial (149) or marine (78) but the ciliates of soils (106 species) are the best studied. These mostly live in layers of slightly decomposed litter, where abundances of up to 10 000 individuals per gram of dry mass of litter are achieved. They are mostly bacterivores (39%), predators (34%), or omnivores (20%). The remaining species are fungal feeders or anaerobes. About 70% of soil species are cosmopolitan. Perhaps surprisingly, soil and freshwater habitats have few species in common.

Ciliates are important inhabitants of the guts of herbivores, especially the rumen and reticulum of ruminants. Most are involved in the digestion of the same plant materials as the rumen bacteria with which they compete and ingest. They make up a large proportion of the microbial biomass in the rumen and contribute 50% or more of total microbial fermentation products. Interestingly, defaunation experiments involving chemical removal of the ciliate fauna have shown that they are not essential for the survival and normal functioning of the host. Notwithstanding, there is a known connection between rumen ciliates and the methanogenic bacteria (particularly archaeobacteria) that live on their surface or within their cells (Tokura et al. 1999), transferring genes to their hosts (Ricard et al. 2006). *Balantidium coli*, a common inhabitant of the guts of pigs worldwide, sporadically causes gut ulceration and clinical enteritis in New Zealand pigs.

In the marine environment, a large number of free-living ciliates inhabit benthic sediments but nothing is known about the fauna. On the other hand, the pelagic tintinnids, loricate members of the plankton, have been studied and the fauna is fairly well characterised. Other common planktonic ciliates are *Cyclotrichium meunieri* and *Mesodinium rubrum*, which cause harmless seasonal red-water blooms in harbours and coastal waters. Many species have commensal and parasitic relationships with a variety of marine organisms. The most problematic are those that cause diseases of fishes. *Ichthyophthirius multifiliis*, often associated with ornamental fishes, can cause significant losses in eel culture. *Cryptocaryon irritans* has been observed in captive snapper and species of *Trichodina* can affect several species of fin fish if confined in conditions that promote susceptibility; wild fish can be affected as well, but do not normally manifest actual disease (trichodiniasis) (Foissner et al. 2012).

## PLANTAE

Molecular evidence for a single origin for red-algal, green-algal and glaucophyte plastids is supported by the structure of plastid genomes and the light-harvesting complex. Accordingly, the plant kingdom sensibly includes not only land plants but glaucophyte, red and green algae (Cavalier-Smith 1998, 2004, 2010b), in contradistinction to the treatments of Margulis and Schwartz

(2001) and Adl et al. (2005), who restricted Plantae to land plants. Six phyla are recognised here: Glaucophyta, Rhodophyta, Chlorophyta, Charophyta, Bryophyta, and Tracheophyta. Total New Zealand plant diversity is 7555 species (Table 1).

### Algal plants

Glaucophyta globally contains only eight genera of freshwater algae that exist as flagellate unicells or small colonies of up to 16 cells. Only temperate-cosmopolitan *Glaucocystis nostochinearum* is known from New Zealand, found in a boggy pool of unknown location in the South Island (Skuja 1976; Broady 2012).

Rhodophyta (red algae), on the other hand, are diverse in New Zealand, with 541 species (89 unnamed) listed by Nelson (2012). All but 20 are marine. The marine species are found from the high to middle intertidal zone to deep coastal waters (200 metres at the Kermadec Islands) where there is sufficient penetration of sunlight to allow photosynthesis to occur. Although red seaweeds do not grow as large as brown seaweeds, they display a very wide range of growth forms, produce considerable biomass, create major habitat in the shallow subtidal and provide food for a range of marine organisms (and humans). A few filamentous species penetrate other organisms, including *Neevea repens* (not listed in Nelson (2012)) in sea squirt tunics (Lambert et al. 1996). Some rhodophytes are calcified, including turfing coralline algae and their non-branching relatives that form unattached growths (rhodoliths) resembling small corals. Rhodolith beds (maerl) provide a specialised habitat and have been linked to the settlement and development of invertebrates such as paua (Nelson 2009). Fifteen red-algal species are alien. Most have a restricted distribution. One forms substantial biomass in the Auckland area.

Filamentous freshwater species may be found in oligotrophic springs and other water bodies where their presence is a good indicator of water quality. *Chroodactylum ornatum* is a species of brackish water and is common in parts of the lower Clutha River. *Cyanidium caldarium*, on the other hand, is an extremophile. A member of subphylum Cyanidiophytina, it has been recorded from volcanoes, hot springs, and acidic soils around the world and is found at a number of thermal sites in the North Island. Cyanidiophytes are the only eukaryotes known to survive extreme acidophilic/thermophilic habitats (pH 0.5–3, with temperatures to 56°C).

Red algae are the only source of carrageenans and agars, which have wide use in food products and various industrial and pharmaceutical applications. In New Zealand, harvest of wild stocks of *Pterocladia lucida* and *Pterocladia capillacea* for these compounds has occurred for more than 60 years. In fact, New Zealand has one of the most diverse floras of carrageenan-containing algae in the world and research continues on the polysaccharide chemistry of selected taxa. New Zealand also has a very diverse flora of seaweeds related to the species cultivated to wrap sushi. Known as karengo by Māori, the species are listed as a taonga in the Ngāi Tahu Deed of Settlement. Research continues on the life histories and taxonomy of karengo species and relatives (Sutherland et al. 2011), particularly in relation to sustainable harvesting of wild stocks and the potential for aquaculture.

Green algae in New Zealand comprise at least 1119 species (and 255 infraspecific taxa) (Broady et al. 2012). They range in size from tiny unicells about a micrometre in diameter to complex, structurally differentiated plant bodies 60 centimetres high with stems, branchlets and anchoring rhizoids (stoneworts). Two phyla encompass green algae – the Chlorophyta and, depending on

phylogenomic parsing, Streptophyta or Charophyta. Streptophyta is a name (often used as a phylum) given to the clade that includes charophytes and the derivative land plants. As used in this chapter, Charophyta is a paraphyletic taxon that includes the ancestor of a monophyletic phylum Bryophyta. Phylum Tracheophyta comprises vascular plants.

The chlorophyte clade is also known as the UTC clade, referring to the major classes Ulvophyceae, Trebouxiophyceae and Chlorophyceae, but three or four additional classes, mostly of unicells, are also included. Ecologically, green algae are found from alpine snows (snow algae) to 70 metres deep at the Kermadec Islands and in ocean plankton, in a range of fresh, brackish and saline waters, as well as in soils or as crusts on rocks, fences and walls of houses and buildings, as epiphytes on plant leaves, as symbionts of lichens, some protists and lower animals, as endophytes of rock, shell and living organisms (Lambert et al. 1996) and even as parasites of insects and vertebrates. Accordingly, they have a range of important ecological roles in trophic webs and in structuring aquatic habitats and biotopes. Even in soils, green algae (as unicells and simple filamentous and colonial forms) can fix at least 80 kilograms of carbon per hectare per year. Broady et al. (2012) have reviewed the many applications of green algae in human technology (as dried biomass or extracts for human and animal food or supplements, energy production from biofuels, use in sewage-oxidation ponds, bioremediation, etc.). Some filamentous species, native and alien, can respond to nutrient enrichment of flowing fresh waters, forming extensive growths that can impede water flow in streams, irrigation channels and drainage ditches. Blooms of planktonic green algae in nutrient-enriched lakes can also cause oxygen deficits and taint drinking water, especially upon their death and decay.

Freshwater desmids (Charophyta) comprise 46% of the total green-algal species diversity in New Zealand, with 34 endemic species. Even though the group has been widely collected and studied in New Zealand it is recognised that knowledge of likely actual diversity is still incomplete. They have no current economic value but have potential as indicators of water quality. Most prefer oligotrophic or mesotrophic situations in which the calcium content is low and pH is neutral. Some 18 species of Characeae are recognised in New Zealand. They are found in a range of fresh waters from still to flowing and even brackish. Most prefer clear, low-productivity water bodies. Species of *Nitella* and *Chara* are the most ubiquitous indigenous plants of the submerged flora of lakes and ponds, contributing to diverse species-rich floral assemblages at the margins of lakes or at the mid-depth range, but Characeae can form extensive meadows beyond the depth limit (10 metres) of vascular plants. Such meadows comprise the deepest vegetation in deep clear lakes, to depths of 34 metres or more. More details on these groups and accounts of green algae in lake phytoplankton and aquatic periphyton are given in Broady et al. (2012).

In the marine environment, there are far fewer green seaweeds and planktonic chlorophytes (there are no marine charophytes) than there are in fresh water. One planktonic species, *Halosphaera viridis*, can be so abundant in the open ocean that it is an important food source for planktonic and nektonic organisms like larvae of the commercial fish *Macruronus novaezelandiae* (hoki). The best-known macroalgal genera include *Bryopsis*, *Caulerpa* and *Codium* (Bryopsidales), *Chaetomorpha* and *Cladophora* (Cladophorales), *Monostroma* (Ulotrichales) and *Ulva* (including *Enteromorpha*) (Ulvales). The latter genus is tolerant of salinity variations in estuaries and can grow abundantly in some harbours

subject to human influence as a kind of 'green tide'. There is no commercial use of green seaweeds in New Zealand but some marine-farming sites have been licensed for farming *Ulva* (as sea lettuce). Ten green seaweed species have been introduced to New Zealand but the impact and risk posed by them is far from clear.

There are only two species of strictly marine angiosperms in New Zealand, the seagrass *Zostera muelleri* and mangrove *Avicennia marina* (mānawa). Seagrass can form extensive meadows from just above low tide to 2 metres depth. Its stems creep beneath the mud and become so interwoven with those of adjacent plants that a firm mat develops, stabilising the sediment. Seagrass meadows enhance primary production and nutrient cycling, elevate biodiversity and provide nursery and feeding grounds for a range of invertebrates and fish. Mangrove covers about 22 500 hectares, less than 0.1% of New Zealand's land area, from Kawhia and Ohiwa Harbour northward. Its shrubs and forests contribute to marine food webs through production of detritus, and several marine organisms spend all or part of their life cycles there. Cordgrass (a *Spartina* hybrid) was planted at the Manawatu river mouth in 1913, quickly forming intertidal meadows that trapped sediment with such efficiency that the estuary bed quickly built up, changing the environment from bare tidal flat to pasture. It and two other introduced species spread to many estuaries around New Zealand. They are now classified as noxious and are being eradicated.

#### Land plants

Bryophytes (hornworts, liverworts, and mosses) comprise 1124 described species in New Zealand. All but 35 species are terrestrial. It is a rich flora. For example, New Zealand is arguably the most important 'hotspot' of liverwort diversity in the world from the perspectives of species density, degree of endemism and the presence of a strong archaic element. New Zealand has more species than the whole of Europe and the highest density of species for any country for which a recent checklist is available (Glenny and Fife 2012). New Zealand's hornwort and liverwort flora (606 species) is also remarkable for its size in relation to the vascular-plant flora. There is one endemic family (Jubulopsidaceae). There are only six alien species. Pharmacological studies have been conducted on some New Zealand liverworts to find bactericides and fungicides.

Mosses, too, are a sizeable fraction of the New Zealand flora (517 species) and occupy many of the same habitats as hepatics and hornworts although there are far more species (30) in fresh water. On a proportional basis, New Zealand has fewer species than the United Kingdom and Ireland (692 species). Some 22.6% of indigenous moss species are endemic (compared to 47% for hepatics and hornworts). There are nine endemic moss genera (cf. 14 hepatic genera) but no endemic families. There are 31 alien species. These mostly inhabit soil in disturbed areas or are found among grasses and herbs in waste areas, lanes and road verges.

Bryophytes comprise a significant part of the diversity and biomass of the wetter New Zealand forests, especially as ground flora (the epiphytic flora is not as well developed as in the wet tropics), hence they play a significant ecosystem-service role in forest catchments, being regarded as 'water-purification plants' for the removal of atmospheric particulates. One native species, *Sphagnum cristatum*, is commercially harvested as peat moss.

The phylum Tracheophyta (the vascular plants) comprises lycophytes, ferns and related taxa, and seed plants (conifers and flowering plants). The phylum is the most species-rich of

all green-plant lineages, making up our forests, grasslands, and croplands. Seeds, and the fruits that contain them, are critically important for the sustenance of humanity, not to mention much other terrestrial life. All the staple grains, for example, rice, wheat, and barley, are one-seeded fruits. But seed plants also provide construction materials, paper, medicines, clothing and ornamental plants. Forests, grasslands and wetlands provide numerous ecosystem services of benefit to humans (see other chapters in this volume) and contribute massively in the conversion of sunlight into chemical energy and provision of atmospheric oxygen.

Including naturalised-alien species there are 4749 tracheophyte species, of which 2222 named species (2026 seed plants) are indigenous and 1735 endemic. The endemic component, particularly of seed plants (81%), makes New Zealand one of the global hotspots for floral endemism. All 20 species of indigenous gymnosperms are endemic and there are 50 endemic seed-plant genera (Breitwieser et al. 2012) and three endemic fern genera but no endemic families. There are 13 native lycophyte species and 182 native ferns (including whisk ferns or Psilotales). New Zealand has representatives of 1249 genera and 204 families of angiosperms; almost half the families are represented by only a single genus. In terms of indigenous species, the largest angiosperm family is the Asteraceae (Compositae) with 292 species, followed by the Poaceae (Gramineae) (188 species), Cyperaceae (178 species) and Plantaginaceae (153 species); in terms of naturalised-alien species, the ranks are: Poaceae (267), Asteraceae (252), Fabaceae (Leguminosae) (155), and Rosaceae (117). New Zealand's seed-plant flora shows a number of unusual features, such as a high proportion of species with separate male and female individuals, possibly linked to the unspecialised pollinator fauna. Godley (1975, 1979) showed that a high proportion of this gender dimorphism had probably not evolved in New Zealand, leading Lloyd (1985) to propose that immigrant selection was involved in about 85% of the examples of the evolution of New Zealand's unisexual plant groups. Other features include many species with small, white or drab, short-tubed actinomorphic flowers, and growth forms adapted to particular habitats (e.g. alpine cushion plants, mountain scree plants, lowland divaricating plants). There are relatively few annuals, deciduous plants or geophytes.

Native plants have featured in Māori traditional uses as sources of foods, medicinal herbs and drugs, fibres for weaving and building materials and as having artistic or other cultural significance (e.g. Brooker et al. 1987; Crowe 1990; Cooper and Cambie 1991; Riley 1994; Scheele and Walls 1994). Several native species are currently harvested casually or used commercially as supplementary foods and as herbs and flavourings in condiments and beverages (see King et al., this volume). Horticultural and arable crop diversity is also reviewed elsewhere in this volume.

Much current research on plant biosystematics in New Zealand aims to understand evolutionary processes and relationships. Phylogenetic and phylogenomic studies are clarifying the origins of the native flora in relation to past geological history, including the Late Oligocene inundation of the New Zealand landmass, the rise of the Southern Alps and glaciations, and vicariance and/or dispersal biogeographic hypotheses. Breitwieser et al. (2012) summarise the taxa that have received attention during the past two decades, especially the 2000s. Remarkably, some 15–20% of the known native seed plants are still undescribed or need to be critically examined.

## FUNGI

Fungi is the most speciose non-animal eukaryote kingdom in New Zealand. Some 8395 species are known (including 350 known-undescribed species and 1993 naturalised-alien species) (Buchanan et al. 2012a), but the estimated total for New Zealand, once all species have been discovered, approaches 32 000 (including Microsporidia) (Table 1). Some 26% of the indigenous mycota is endemic. Fungi are associated with almost all forms of life and contribute to ecosystems in myriad ways – living saprobically on dead organic matter or symbiotically in association with living cells of other organisms. The latter may be mutually beneficial (mutualistic, e.g. lichens, mycorrhizas), benign or non-harmful to either partner (commensal, e.g. endophytes in living plant tissues), or harmful to the other partner (parasitic, e.g. animal and plant parasites, mycoparasites). Symbiotic association with plant roots as mycorrhizas is one of the keys to the evolutionary success of land plants. Fungi are also important in human affairs – used as food and in industry (e.g. yeasts) and medicine (see McKenzie (2004), Buchanan et al. (2012a) and Beever et al. (2012b) for New Zealand examples of these uses), in biodegradation, as mycotoxins, as sources of disease and for their roles in ecosystems.

Plant-pathogenic fungi cost New Zealand growers, gardeners, foresters and farmers millions of dollars in annual loss (through reduced quality and yields and increased production costs). Pathogens can be found in all groups of fungi. Most diseases of exotic crop, pasture and forest plants are caused by alien fungi, many of which were introduced accidentally with the host plant before the realisation of the importance of plant quarantine. This is particularly the case with rusts and smuts (phylum Basidiomycota) (Buchanan et al. 2012b), but some native species can infect exotic plants and insects can be vectors also.

Endophytic fungi exist symptomless within plants but may include latent pathogens that cause disease only under specific environmental conditions. Endophytes occur in most plants studied to date and in all major plant organs such as leaves, stems, and roots. The relationship between plant and fungus is not well understood for many groups of plants but may be mutual or commensal. In New Zealand, endophytes of grasses have received much attention owing to their major impact on the performance of pastures. Usually the association is mutualistic, with the host grass able to benefit from endophyte presence through reduced herbivore feeding, increased resistance to insects, improved plant growth, and possibly disease resistance. However, endophytes in grasses are also associated with a number of animal toxicoses including ryegrass staggers and fescue toxicosis.

Mycorrhizal associations in New Zealand are mostly of the vesicular-arbuscular type, important to forest trees, for example. The fungal partners are members of the Glomerales (Glomeromycota) (Buchanan 2012), which can have a broad host range (even including liverworts). The fungus assists nutrient and water uptake in the host, by hyphal capture from the surrounding soil of immobile nutrients such as phosphorus, and may also aid the host by providing protection against drought and pathogens. In return, the fungus obtains carbohydrates from the host.

The saprobic role of fungi is of critical importance in the degradation of wood, litter and other organic matter in terrestrial and aquatic habitats. Along with wood-degrading ascomycetes and agarics, non-gilled basidiomycetes are the main agents of decomposition and nutrient cycling of wood in forests. Some species of New Zealand wood-decay fungi are cosmopolitan, but many species are endemic or indigenous. Depending on

the type of enzymatic degradation, wood-decomposing basidiomycete species cause either a white rot, in which the fungus degrades cellulose, hemicellulose, and lignin from the wood cell wall, or a brown rot, where the lignin remains largely intact. White-rot species are more common, with brown-rot species mostly associated with gymnospermous hosts (like untreated radiata pine). Stahlhut (2008) isolated fungi from leaky buildings in New Zealand. The species encountered with the greatest frequency – the basidiomycetes *Gloeophyllum sepiarium*, *G. trabeum*, *Oligoporus placenta* and *Antrodia sinuosa* – represented only 10% of all samples, indicating that leaky buildings support high fungal diversity. Litter decomposers include micro-fungi and larger fungi, which form mycelial mats within litter layers. Litter fungi are highly diverse and include, in particular, anamorphic (asexual stage) ascomycetes and zygomycetes, especially Mucorales. Chytridiomycetes in soils have specialised abilities to metabolise polymers such as chitin, keratin, and cellulose and to decay plant pollen. Some saprobic chytrids may be particularly abundant; *Karlingia rosea* was reported to be the most common chytrid in New Zealand, found in almost 95% of 140 soils sampled from throughout the country (Karling 1968).

Additional species found in houses sampled for mould and mildew include the ascomycetes *Alternaria alternata*, *Aspergillus fumigatus*, *Cladosporium herbarum* and *Stachybotrys chartarum*, which have been implicated in respiratory symptoms in humans overseas (Wilson et al. 2007). Other species of *Aspergillus* and *Pneumocystis jiroveci* also cause pulmonary opportunistic mycoses in humans and *A. nidulans* can affect a variety of native and exotic birds and cause placentitis and abortion in cattle. Buchanan et al. (2012) summarise these and other examples of fungi affecting vertebrates, including dermatophytes (which colonise skin and nails), and mycotoxic species (like *Aspergillus flavus*, which produces the liver carcinogen aflatoxin, and *Pithomyces chartarum*, which causes facial eczema in sheep). Altogether, more than 90 fungal species affect human and animal health. Malone and Charleston (2012) summarise what is known about Microsporidia in New Zealand, a group of minute spore-forming obligate parasites that used to be classified as protozoans. They infect a wide range of invertebrate phyla, some alveolate chromists, vertebrates and, opportunistically, immunocompromised humans.

Entomogenous fungi are associated with insects, the most conspicuous being vegetable caterpillars of the ascomycete genus *Cordyceps*. Some other ascomycetes of the order Laboulbeniales live ectoparasitically on arthropods and there are many examples of fungal-animal associations that involve other fungal groups such as Chytridiomycota and Zygomycota. Buchanan et al. (2012a) summarise examples of these and several other ecological groups in New Zealand involving animals, including dung and ammonia fungi, truffles and truffle-like fungi, predacious fungi and sooty-mould fungi.

The majority of fungi are terrestrial but they can be common (but not speciose) in fresh water (191 species) and are known from the marine environment (89 species) in New Zealand (Buchanan et al. 2012a). Many aquatic (Ingoldian) fungi are ascomycetes and their anamorphs, most of which have spores adapted in shape for dispersal in an aquatic habitat. Aero-aquatic fungi grow underwater but produce their spores in the air. Fresh water is also the main habitat of many Chytridiomycota (Beever et al. 2012a). Most genera isolated from the marine environment are thought to be facultatively marine, being originally terrestrial but able to grow in marine conditions. Some marine fungi may have

significant ecological roles. For example, as parasites of algae, chytridiomycetes are implicated in control of phytoplankton population levels. The chytrid fungus *Batrachochytrium dendrobatidis*, which has caused declines in amphibian populations around the world, appears to be the cause of chytridiomycosis in New Zealand native frogs also (Bishop et al. 2009).

Some 1767 fungal species in New Zealand are lichenised (Galloway 2012), i.e. comprising fungal-algal unions that constitute ecologically obligate stable mutualisms that benefit both partners. The name of the lichen pertains to the fungal partner, most of which belong to the ascomycete class Lecoranomycetes; some are basidiomycetes. Because of their sensitivity to environmental perturbations, lichens have wide applications as biomonitors, particularly of atmospheric pollution (see Daly (1970) and Johnson et al. (1998) for New Zealand potential). Galloway (2008) has reviewed local and regional lichen-based studies relating to climate change, nutrient cycling, and soil consolidation.

## ANIMALIA

The animal kingdom is far and away the most biodiverse of eukaryote kingdoms. The fundamental morphological design (bauplan) of the 31 phyla represented in New Zealand is so variably successful in evolutionary terms – such as the propensity for speciation and adaptation – that some phyla are represented (globally, let alone in New Zealand) by fewer than five named species, whereas the insects alone (one of the classes of Arthropoda) may have as many as a million named species globally. In New Zealand, Coleoptera (beetles) is the single most speciose order of eukaryotes, with at least 5087 named species and possibly as many as 3000 or more undescribed species.

### Terrestrial fauna

The land is the most biodiverse macroenvironment for Animalia. But whereas this is true of New Zealand's animal species (~56% are terrestrial), it is not true of phyla. Of the 31 animal phyla represented in New Zealand, only 10 are found on land whereas all but one are found in the sea (Table 2). Since phyla represent the extremes of genetic diversity, it is in the sea that we find the greatest genetic distance and more high-level taxa, while there is much greater species differentiation on land. Theoretically, it is possible to have high genetic diversity and low species diversity in a particular habitat and, alternatively, low genetic diversity and high species diversity; a large number of species could belong to just a handful of genera in one or two families of a similar type of organism.

The six most speciose (>100 species) truly terrestrial phyla (i.e. not confined to water films or seepages) in New Zealand are Arthropoda (Table 3; 17 476–17 639 terrestrial species, mostly Coleoptera, Diptera, Lepidoptera, Araneae, Hymenoptera, Acari and Hemiptera, all of which have in excess of 1000 species each), Mollusca (906 species of mostly pulmonate Gastropoda), Nematoda (540 species in soil or terrestrial hosts), Chordata (Table 4; 265 terrestrial species, mostly birds and reptiles), Annelida (207 species, comprising oligochaete earthworms and a few leeches) and Platyhelminthes (137 species of land planarians) (Gordon 2009, 2010).

The enormously successful arthropod subphylum Hexapoda includes classes Insecta (having only 11 abdominal segments), Protura, Collembola, and Diplura (the latter three may depart from this number of abdominal segments). Hexapoda are widely and abundantly represented in all of New Zealand's terrestrial

**TABLE 2** Species diversity of New Zealand Animalia (figures slightly modified from Gordon 2009, 2010)

Phylum	Described	Known undescr./ undet.	Estimated undisc.	Terrestrial	Marine	Freshwater	Endemic	Adventive
Porifera	512	263	500	0	770	5	366	0
Ctenophora	15	4	15	0	19	0	5	0
Cnidaria	812	315	1230	0	1113	14	242	24
Platyhelminthes	396	141	830	137	324	78	199	35
Dicyemida	5	1	50	0	6	0	6	0
Gastrotricha	0	5	25	0	4	1	0	0
Gnathifera	486	44	80	2	44	484	19	0*
Annelida	793	270	775	207	793	55	436	80
Orthonectida	0	1	3	0	1	0	1	0
Sipuncula	26	0	5	0	26	0	2	0
Mollusca	2895	1695	430	906	3595	89	3880	50
Nemertea	37	30	140	6	57	4	28	0
Brachiopoda	45	5	2	0	50	0	43	0
Phoronida	3	0	3	0	3	0	0	0
Bryozoa	631	331	300	0	954	8	582	24
Kamptozoa	6	7	25	0	13	0	2	1
Chaetognatha	14	1	25	0	15	0	0	0
Tardigrada	85	3	100	83	5	83	25	0*
Onychophora	9	25	10	34	0	0	34	0
Arthropoda	18 144	3548–3714	25 125– 28 065	17 476– 17 639	2978	1248	16 207– 16 221	1773
Kinorhyncha	6	39	30	0	45	0	6	0
Priapulida	3	1	4	0	4	0	0	0
Loricifera	0	4	10	0	4	0	2	0
Nematoda	710	1250	4500	540	1410	>9	90	152
Nematomorpha	5	0	2	0	1	4	4	0
Xenacoelomorpha	2	0	40	0	2	0	1	0
Echinodermata	566	70	45	0	636	0	246	0
Hemichordata	5	2	4	0	7	0	1	0
Cephalochordata	1	0	0	0	1	0	1	0
Tunicata	190	3	195	0	193	0	125	12
Chordata	1572	211	835	264	1427	96	469	96
			35 340	19 660	14 500	2169	23 022– 23 036	2247

Phyla are listed according to major groupings (clades). Note that for major-habitat tallies (terrestrial, marine, freshwater) some species occur in more one column.

\* Not easily determinable

**TABLE 3** Species diversity of New Zealand Arthropoda (figures slightly modified from Gordon 2010)

Subphylum	Described	Known undescr./ undet.	Estimated undisc.	Terrestrial	Marine	Freshwater	Endemic	Adventive
Chelicerata	2848	704	15 130– 16280	3275	115	158	2695	114
Myriapoda	164	131	200	295	0	0	266	28
Crustacea	2528	485	5060	123	2655	236	1124	46
Hexapoda	12 598	2228–2394	4735–6525	13 783– 13 946	197	854	12 122– 12 136	1585
Totals	18 144	3548–3714	25 125– 28 065	17 476– 17 639	2967	1248	16 207– 16 221	1773

Note that for major-habitat tallies (terrestrial, marine, freshwater) some species occur in more one column

TABLE 4 Species diversity of New Zealand Chordata (figures slightly modified from Gordon 2009)

Subphylum	Described	Known undescr./undet.	Estimated undisc.	Terrestrial	Marine	Freshwater	Endemic	Adventive
Myxini	8	0	0	0	8	0	5	0
Cephalaspidomorphi	1	0	0	0	1	1	0	0
Chondrichthyes	124	24	30	0	148	0	29	0
Actinopterygii	1241	50	450	0	1233	58	193	22
Amphibia	10	0	0	4	0	4	4	3
Reptilia	87	10	5	89	7 <sup>▲</sup>	0	88	1
Aves*	281	5	3	137	122	35	144*	38
Mammalia	78	0	0	35	48	0	6	32
Totals	1830	89	488	265	1567	98	469	96

<sup>▲</sup> Seasonal non-breeding species.

\* Includes 55 species extinguished since human colonisation. Original residents comprised 213 species

Note that for major-habitat tallies (terrestrial, marine, freshwater) some species occur in more one column

habitats. Scavenging species help recycle dead organic material; insects in soil litter are responsible for much of the process whereby topsoil is made. Although many species are major pests, parasitising livestock and causing damage to crops and stored products, others are profoundly beneficial as pollinators of economic crops or sources of products like honey. Macfarlane et al. (2010) review what is known of New Zealand's hexapod diversity, giving an order-by-order account, including their ecological and economic impacts. More recent revisions update certain taxa, for example Simuliidae (Craig et al. 2012) and part of Carabidae (Laroche and Larivière 2013). Groups with the highest numbers of endemic species (more than 200) are Coleoptera (>5027 species), Diptera (>3032 species), Lepidoptera (1389 species), Hemiptera (826 species), Hymenoptera (742 species), Collembola (266 species) and Trichoptera (241 species). The groups with the highest numbers of naturalised-alien species (more than 50) are Coleoptera (418 species), Hemiptera (280 species), Hymenoptera (259 species) Diptera (195 species), Lepidoptera (139 species), Phthiraptera (90 species) and Thysanoptera (55 species).

Protura (18 species, 10 endemic), Collembola (346 species, 266 endemic) and Diplura (10 species, six endemic) are diminutive hexapods that have not been fully described. This is especially true of the Collembola, which, in spite of earlier studies and revised synonymies, has a much greater diversity in New Zealand as indicated by collections. These detritus feeders play an important role in nutrient cycling but can be found in a variety of habitats. The largest of the 16 families (in three orders) are Entomobryidae (98 species), Isotomidae (87) and Katiannidae (51). Nearly 80% of the species and 20% of the genera are endemic.

Archaeognatha (bristletails), the most ancient of the terrestrial insect orders, is represented by two endemic species of *Nesomachilis*. Weta (Orthoptera) are one of the icons of New Zealand, classified in two families – Anostostomatidae (tree and ground weta, with 29 described and >33 known-undescribed species) and Rhaphidophoridae (cave or jumping weta, with 54 described and >30 known-undescribed species). Neither family is endemic but all New Zealand genera (22 among the two families) and species are. A species of *Deinacrida* is the world's heaviest adult insect. All 31 species of native cockroaches (Blattodea) are endemic. There are only nine species of termites (Isoptera), including three endemic species and possibly five adventive. One of the two species of Mantodea (praying mantises) is endemic and perhaps 13 of the 21 species of earwigs (Dermaptera). There

are no endemic genera in these three latter orders. On a proportional basis, New Zealand's Phasmatodea are notable for their exceptional level of endemism. All 29 species are endemic and probably all 9 genera, once a revision of *Clitarchus* is complete. The 65 native thrips species (Thysanoptera) and 11 genera are endemic. The order includes many pest species, including, ironically, the endemic flower thrips, *Thrips obscuratus*, which, unlike many native species that have a single host, is found on at least 225 host species and is a major pest of introduced plants including horticultural crops. Psocoptera (booklice and barklice) is a little-studied group and many more species are expected. Affinities are mainly with Australia and partly also New Caledonia. There are only 69 species, including 31 endemic and 5 adventive. The Bryopsocidae is endemic. One of the three endemic genera is monotypic *Sandropsocus*, restricted to the Bounty Islands. Phthiraptera (lice) comprises 350 species, only 29 (~8%) of which are endemic, along with one genus and two subgenera; most of the fauna parasitises birds. There are 26 species of fleas (Siphonaptera), including 17 endemic species and no endemic genera. As with lice, they mostly parasitise birds.

Not surprisingly the highest numbers of endemic genera are to be found in the largest orders – Coleoptera 539, Diptera 192, Lepidoptera 140, Hemiptera 119, Hymenoptera 55. Hemiptera has the dubious distinction of including more destructive and costly pest species than any other insect order globally and there are a large number of problem species in New Zealand as well. In suborder Sternorrhyncha these include, among others, Psylloidea (jumping plant lice, with a number of endemic species on native plant hosts), Aleyrodoidea (white flies, with 8 endemic species), Aphidoidea (aphids, 127 species, with only about 12 endemic) and Coccoidea (scale insects, ~390 species, of which ~318 are endemic). Among the Coccoidea, New Zealand is relatively rich in Eriococcidae, with 94% endemism. One family, Phenacoleachiidae, is wholly endemic, and probably all New Zealand species of Coccidae. New Zealand aphids constitute a distinct taxonomic component. *Neophyllaphis* and *Sensoriaphis* are primitive genera with Gondwanan distributions; *Neophyllaphis* is considered to be the closest living relative to the ancestral aphid form. The hemipteran suborder Auchenorrhyncha is a highly diverse clade that includes the cicadas, spittlebugs, leafhoppers, treehoppers, and planthoppers, comprising a major component of the plant-feeding insect fauna in New Zealand. Some 27 of the 69 genera of Auchenorrhyncha are endemic and



159 of the 195 species. Three of the five genera and all 34 species of cicadas (Cicadidae) are endemic, as are 9 of the 11 genera and all 26 species of Cixiidae (cixiid planthoppers). Both genera and all 16 species of Myerslopiidae (ground-dwelling leafhoppers) are endemic as are the sole species of the planthopper families Derbidae and Dictyopharidae. The moss bugs (Peloridiidae, suborder Coleorrhyncha) appear to be a relict Gondwanan group. The three New Zealand genera and all nine species are endemic. Some 55 of the 136 genera and 249 of the 305 species of suborder Heteroptera are endemic. There are 28 families, the largest of which are the plant bugs (Miridae, 120 species or 39% of the fauna), rhyarochromid seed bugs (42 species), flat bugs (Aradidae, 39 species), and lygaeid seed bugs (33 species). The faunal affinities and other attributes are reviewed in Macfarlane et al. (2010).

The four most speciose of the 89 beetle (Coleoptera) families in New Zealand account for ~60% of the 5087 known species. They are the rove beetles (Staphylinidae, 1232 species), weevils (Curculionidae, 1225), ground beetles (Carabidae, 585), and Zopheridae (no one common name) (191). The least diverse families (eight of them) have just one endemic species each, three of them comprising monotypic genera that may be primitive members of their group. There is only one endemic family (Cyclaxyridae), but a number of lineages have clear Gondwanan affinities. Ecological roles and economic aspects are briefly reviewed in Macfarlane et al. (2010) but the biology of most species is not known. Coccinellids (ladybirds) are used in biocontrol of aphids, mites, and scale insects. A number are wood borers that perform ecologically useful roles or, like introduced *Anobium punctatum*, mine timber and furniture. Almost all (~99.5%) native beetles are endemic, having evolved in isolation in New Zealand or are survivors of groups that have died out overseas. Very few of the native species have adapted to the modified landscapes, pastures, crops and gardens. Of the 5090 total species listed in Macfarlane et al. (2010) and Larochelle and Larivière (2013), 4648 (~91%) are endemic and 418 (~8%) are naturalised aliens.

The diversity of species within the Diptera (flies) is more evenly spread among the 77 families in New Zealand than in the Coleoptera. Eight families account for ~63% of the total fauna of at least 3228 species – crane flies (Tipulidae, 619 species), soldier flies (Stratiomyidae, 283), fungus gnats (Mycetophilidae, 266), gall midges (Cecidomyiidae, 229), tachina flies (Tachinidae, 190), long-legged flies (Dolichopodidae, 147), midges (Chironomidae, 146), and house flies and relatives (Muscidae, 145). About 33% of the genera that existed before European settlement are endemic, a figure 4.7 times higher than that for New Caledonia or Tasmania, and many are monotypic, notably in the Chironomidae. The Tachinidae is particularly noteworthy in having the highest numbers of endemic genera (90%) and species (83%). The only endemic family is the Huttoninidae, with two genera (sometimes included in the Sciomyzidae), but the family status of *Starkomyia inexpecta* remains unresolved within Mycetophiloformia. The endemic calliphorid subfamily Mystacinobiinae has a single species, flightless *Mystacinobia zelandica*, which survives on the guano and debris of the New Zealand short-tailed bat. Diptera in New Zealand have a wide variety of ecological roles, comprehensively summarised by Macfarlane et al. (2010); pests account for only 0.5% of species. Beneficial roles include pollination, biocontrol of noxious weeds, vegetation recycling, removers of carrion and dung, and as food items for other organisms (e.g. birds, reptiles, spiders, other invertebrates). Some are natural enemies of moths and soil pests. Pest species include those that

affect pastures, crops (including cultivated mushrooms) and gardens, mainly as larvae.

New Zealand's hymenopteran fauna is poorly known. At least 1541 species are known but only 721 have been described (as of 2010) and an estimated 610 species remain to be described. There are 47 families, nine of which are solely adventive. Because of lack of detailed knowledge of the fauna and its biogeographic affinities (and hence, genetic distinctiveness), data on endemism are only approximate. A third of the nine species in the paraphyletic suborder Symphyta are endemic (including two species of the endemic xiphydriid genus *Moaxiphia*). All remaining species belong to suborder Apocrita. Some 48% of the genera of Mymaridae (superfamily Chalcidoidea) are endemic but the high number of undetermined species precludes giving a percentage for the species. All New Zealand species of Gasteruptionidae, Perilampidae, Rotoitidae, Embolemyidae, and Sphecidae are endemic but none of these families has more than seven species. All 35 species and six of the genera of the diapriid subfamily Ambrositrinae are endemic. Maamingiidae, with one genus and two species, is the only endemic family of Hymenoptera. The chalcidoid family Rotoitidae was thought to be endemic until a second genus was recognised from Chile. The most striking features of the native fauna are the paucity of stinging (aculeate) and sawfly/woodfly (symphytan) species and the radiation of certain parasitic groups. Superfamily Cynipoidea (gall wasps and relatives) is very poorly represented. Vespoidea, which includes ants and vespid wasps, is also depauperate, with only 40 species of ants (10 species and the genus *Huberia* endemic, four indigenous and the rest introduced), no native vespids and only 10 endemic pompiliids (one other pompiliid, a mutillid and a scoliid introduced). Of the 61 species of Apoidea (bees), 41 species are endemic, particularly in the basal family Colletidae; there are no native Apidae. Apart from pollinating Apidae and some biocontrol species, the impact of adventive Hymenoptera is overwhelmingly negative, such as the defoliating willow sawfly, some parasitoid species that attack endemic hosts, stinging wasps that also compete with native species for nectar and honeydew, and nuisance ants.

The New Zealand lepidopteran fauna (1490 native and 174 adventive and vagrant species) is not diverse by world standards but has a number of features that make it of interest and importance, including the high level of endemism (>85%), the number of species showing wing reduction and flightlessness, and the representation of primitive groups, including one endemic superfamily (Mnesarchaeoidea, with one genus, seven described species and seven undescribed species), that enhance scientific understanding of lepidopteran evolution. There are 140 endemic genera. As with many of the other large insect orders, the fauna is disharmonious, i.e. there are no native species of some otherwise ubiquitous families while other groups have undergone considerable radiation (Macfarlane et al. 2010). For example, New Zealand is especially rich in Lepidoptera with detritivorous larvae, i.e. those that feed on dead wood, fungi or leaf litter, including 250 species of Oecophorinae (Oecophoridae). All species of Blastodacnidae, Cecidosidae, Copromorphidae, Epermeniidae, Glyphipterygidae, Hepialidae, Micropterigidae, Mnesarchaeidae, Momphidae, Roeslerstammidae, and Thyrididae are endemic. Of these, Hepialidae is largest, with 27 species; six of the genera are endemic. One endemic species of Tineidae (*Archyala opulenta*) has been reared only from larvae feeding on the guano of the short-tailed bat – the only known example amongst the endemic Lepidoptera of a close association with a specific vertebrate

'host.' There are more examples of host specificity among plants, including the endemic monotypic taxon *Houdinia flexilissima*; the larva mines and pupates inside the threatened endemic restiad *Sporanthus ferrugineus*. Ecologically (and economically), a number of species are pollinators, constitute food for a range of predators, cause nuisance leaf-rolling in orchard trees and horticultural plants, compete with stock for spring pasture growth (porina grubs of *Wiseana* species) and defoliate plants (e.g. the white-spotted tussock moth and the painted apple moth, both Lymantriidae, which have been eradicated through costly aircraft spraying campaigns over suburban Auckland).

In order of numerical and species dominance, arachnids in New Zealand are represented by mites and ticks (Acari, ~1450 species), spiders (Araneae, 1700), harvestmen (Opiliones, 237), pseudoscorpions (Pseudoscorpionida, 67 species), and micro whip scorpions (Palpigradi, 3?) (Sirvid et al. 2010). The vast majority of these are terrestrial. Mites comprise at least 614 genera in 197 families and 5 orders, Acari being an infraclass. Owing to the very small size of most and their wide distribution, their diversity in New Zealand is far from known; conservative estimates of undiscovered Acari species suggest at least another 14 000. The distribution of known species among the orders is quite uneven – Trombidiformes (exclusively suborder Prostigmata) 660, Sarcoptiformes 598, Holothyrida 1, Ixodida 11, Mesostigmata 178. The distribution of taxon richness among families is also very patchy, with few large families but many small ones. On average, there are about seven species per family. Of the 188 families, 141 or three-quarters of them have seven or fewer species. The 10 largest families are Eriophyidae (126 species), Oppiidae (89), Aturidae (68), Stigmaeidae (65), Phytoseiidae (35), Tetranychidae (35), Ologamasidae (29), Acaridae (28), Halacaridae (28) and Tenuipalpidae (27). These 10 families alone account for 38% of all the species. The sizes of the Eriophyidae, Tetranychidae, Tenuipalpidae, Phytoseiidae, and Stigmaeidae are relatively large, but this may not be simply because they are more diverse than other families. Instead it could result from more studies on these mites owing to their economic importance as pests or natural enemies of pests. For most of the groups that have been well studied, endemism is high, but precision is confounded by the lack of comparative studies in New Zealand and neighbouring land masses. One-third of the genera and 82% of the species of the sarcoptiform suborder Oribatida are endemic. Some 89% of the 65 Stigmaeidae (Prostigmata) are endemic. The relatively low endemism for spider mites (29%), on the other hand, may be a consequence of the high rates of dispersal of the phytophagous mites and the lack of systematic collection on native plants. Mites have a prodigious range of food preferences and habits, as predators, ectoparasites and animal hitchhikers, plant-eaters and fungal-feeders, and those species attracted to decaying plant material, dung, and dead animal bodies. Not surprisingly, in spite of their small size, mites are important ecologically and economically as pests of crops, food, and horticultural plants, natural enemies of pests, parasites of domestic animals and humans, nutrient recyclers in the food chain, and vectors and agents of diseases. Ticks are among the better-known Acari because of their relatively large size and because they attack humans, domestic animals and native vertebrates. The elongated mites that are specialised for living in hair follicles can be quite harmless but others can cause mange and similar skin disorders in pets and humans by burrowing (like the scabies mite) into the skin. Birds have at least one species of feather mite for each species of bird. Others are blood feeders, like the poultry mite. Plant-feeding

mites have considerable economic importance, particularly as horticultural pests. The New Zealand species include a number of eriophyoid gall mites. Spider mites are also very important plant pests. A few mite species of cosmopolitan distribution cause considerable damage to stored grains and cereal products.

Some 52 of the world's 109 spider families (Araneae) are found in New Zealand. Of the 1700 New Zealand species (547 undescribed), 1628 species (96%) and 137 genera are endemic. Only 38 are adventive. The total fauna could be as high as 3700 species (Platnick 1992), rivalling the continental United States. Spiders are divided into two suborders, Mesothelae (not found in New Zealand and only 87 species globally) and Opisthothelae, the latter containing two infraorders, Mygalomorphae and Araneomorphae. The New Zealand fauna includes the family Gradungulidae (also found in eastern Australia), which has a number of characters that link the two opisthothelina suborders. Only one spider family, Huttoniidae (with one described and 21 undescribed species), is endemic to New Zealand. A number of the families suggest a Gondwanan connection. Ecologically, spiders have an important role in the regulation of insect numbers. *Latrodectus* (widow spider/redback/katipō) is venomous to humans.

All but two of the approximately 257 known species and 23 of the 25 genera of New Zealand harvestmen (Opiliones) are endemic, as is the family Synthetonychidae. At least 100 species await description and perhaps 100 more are likely to be discovered. The 67 known species of New Zealand pseudoscorpions are highly endemic at the species level (60 of the 64 native species) but less so at the genus level (11 of 24), and there are no endemic families. At least another 50–100 species are likely to be discovered, however. The presence of 2–3 species of order Palpigradi has been noted in New Zealand (Forster and Forster 1999) but there appear to be no specimens in collections.

Subphyla Myriapoda is represented by at least 214 species of millipedes (Diplopoda) (but more than 200 additional species are likely to be discovered), 41 species of centipedes (Chilopoda), 20 Pauropoda and 20 Symphyla (Johns 2010). The millipede fauna is typical of the Southern Hemisphere but needs further study. There are 12 described endemic genera and at least another nine undescribed. All of the native species are endemic and there are 13 adventive species. The most speciose family is the Dalodesmidae (111 species, including 60 undescribed); *Icosidesmus* alone has at least 41 species. The centipede fauna is small but reasonably diverse. *Craterostigma*, comprising one New Zealand and one Tasmanian species, is the most archaic centipede taxon, in its own order, Craterostigmida. The genetic pattern of the fauna overall supports a Gondwanan origin, not long-distance dispersal. *Maoriella* (Geophilida) is the only endemic genus. All of the native species of the tiny grub-like pauropods are thought to be endemic but they are rarely seen or studied. With 20 species (16 endemic, 4 adventive), the New Zealand symphylian fauna is relatively rich (13% of the known world-fauna). There are no endemic genera of Pauropoda or Symphyla.

The vast majority of Crustacea in New Zealand are aquatic, especially marine, but there is a terrestrial fauna of some 123 species. These are mostly isopods (slaters, 72 species) and amphipods (hoppers, 47 species) but a species of harpacticoid copepod and an ostracod are known from damp forest litter (Webber et al. 2010). Most terrestrial amphipods belong to the Talitridae, the only amphipod family to have successfully occupied terrestrial habitats worldwide; seven New Zealand genera and 47 species are endemic. All terrestrial isopods belong to the suborder

Oniscidea. Eleven families are represented in New Zealand, two of them adventive. Five genera and 61 species are endemic.

Using morphological criteria, five species of phylum Onychophora (velvet worms, peripatus) are recognised in New Zealand. Four more 'species' have been described on the basis of isozyme electrophoresis but the validity and utility of these taxa is questionable and they are currently being revised as part of a larger treatment. It is estimated that a further 25 species will be described (Gleeson and Ruhberg 2010). The sole family Peripatopsidae is currently represented by two genera – ovoviviparous *Peripatoides* is endemic while oviparous *Ooperipatellus* is also found in Australia. Onychophorans are widely distributed in New Zealand, especially *Peripatoides novaezealandiae*, which may be a complex of species. There are strong affinities of the fauna with Tasmania.

Species of phylum Tardigrada (water bears) are entirely dependent on water for day-to-day existence, their tiny size (generally 0.1–0.5 millimetres) allowing many of these essentially aquatic animals to live in interstitial water in terrestrial habitats, among bryophytes and in damp soil and leaf litter. In New Zealand, foliose lichens provide the most favourable suitable terrestrial habitat (based on numbers of species recovered), followed by mosses, liverworts and hornworts, and fruticose and crustose lichens (Horning et al. 2010). Some 83 non-marine species are found in New Zealand, 25 of them endemic but the chances are high they could be found elsewhere when the faunas of other austral areas are studied.

All the above terrestrial animal phyla belong to the major branch of the animal kingdom known as Ecdysozoa (moulting animals), which also includes Nematoda and related aquatic phyla. The true diversity of Nematoda in New Zealand remains to be determined. At present, the only complete checklist of recorded New Zealand Nematoda (Yeates 2010) has more terrestrial species (540, including parasites) than aquatic (220), but this difference may well be based on insufficient information; literature estimates of the little-studied marine free-living nematodes suggest tens of thousands of undiscovered species. Those that have been studied in New Zealand are strongly biased toward nematodes having an economic impact. Hence the largest ecological categories are parasites of vertebrates including humans (221 species), plant-parasitic nematodes (157 species) and soil nematodes (151 species). Advertisements for drenches represent the greatest public exposure nematodes receive in New Zealand, since these are aimed to purge (in a non-specific way) gastrointestinal nematodes from livestock – there are 29 nematode parasite species of sheep and 27 of cattle. But they also infect a wide range of native vertebrates and invertebrates, crop and horticultural plants and native vegetation as well as occurring free-living in soil. Some of the plant-parasitic species can be vectors of plant viruses. Yeates (2010) reviews all these categories and comments on the scope for future studies. Only four endemic genera have been recognised from the known terrestrial fauna; there is no precision on the number of endemic species.

Additional protostome phyla with terrestrial species include the Gnathifera, Platyhelminthes, Nemertea, Annelida, and Mollusca. Gnathifera includes mostly aquatic organisms like rotifers and lesser jaw worms but the wholly-parasitic thorny-headed worms, Acanthocephala (sometimes recognised as a separate phylum but determined by phylogenomics to be highly modified parasitic rotifers), can have terrestrial hosts. There are two such species in New Zealand. Cosmopolitan *Macracanthorhynchus hirudinaceus* was introduced with the pig; an unidentified species

of *Echinorhynchus* has been found in kiwi (Shiel et al. 2009). The nemertean (ribbon worm) fauna of New Zealand is poorly known but, remarkably for a mostly marine phylum, New Zealand has a total of 10 terrestrial (two supralittoral) and four freshwater species out of a worldwide total of 34 terrestrial and freshwater species (Gibson 2009); the entire phylum has fewer than 2000 named species globally. Three of the terrestrial New Zealand genera and all but one species are endemic.

New Zealand is one of the seven global hotspots for land-planarian (Platyhelminthes) diversity. Some 89 species are known and at least 50 more are estimated to be undiscovered (Johns et al. 2009). There has been much recent interest in terrestrial flatworms owing to the economic impact of the otherwise endemic New Zealand earthworm predator *Arthurdendyus triangulatus*, accidentally introduced to Europe. There are also 10 alien species in New Zealand. The genus *Fyfea* and 77 species are endemic. There are also 48 species of parasitic flatworms in terrestrial hosts in New Zealand, 10 flukes (Trematoda), and 38 tapeworms (Cestoda). Three endemic cestodes parasitise native reptiles, another endemic species occurs in the long-tailed bat and at least 16 species are found in birds, including an endemic species in kiwi and an endemic genus and species (*Pulluterina nestoris*) in kea. All other species are parasites of livestock. Trematodes affect livestock and some native birds, a reptile and a species of the more-or-less terrestrial amphibian *Leiopelma archeyi* (Archey's frog).

Terrestrial Annelida include 201 species of earthworms and four species of leeches (Glasby et al. 2009). New Zealand earthworms belong to suborder Lumbricina of the clitellate order Haplotaxida; there are also some terrestrial species of suborder Tubificina. Some 165 species and 13 genera are endemic, all belonging to Lumbricina. Adventive species of Lumbricina number 24 and there are 8 adventive terrestrial Tubificida. The greatest native diversity belongs to the Acanthodrilidae. The soils of those regions of New Zealand that have been transformed for pastoral farming, crop production or gardening are now populated by exotic species, mainly of European origin, mostly Lumbricidae. There can be competitive replacement of native species by exotic species following disturbance of native habitat. Native earthworms will not generally survive for long in remnants of native vegetation less than 30 hectares in area (Lee 1961). The clitellate order Euhirudinea (leeches) is not very diverse in New Zealand. There are only four terrestrial species but two (*Hirudobdella* and *Ornithobdella*) of the three genera (a third genus is uncertain) are endemic. They are almost exclusively confined to the Open Bay Islands, Snares, and Solander Islands where they are associated with seabirds.

Molluscs are represented in the terrestrial environment by a globally distinctive land-snail fauna of about 906 species of which more than 440 species in collections are undescribed (Spencer et al. 2009) and the actual fauna is likely to exceed 1000 species. At the family level, diversity is relatively low (only 11 of the 80-odd families known globally are represented), which is not unusual for a regional fauna, and families that tend to dominate land snail faunas elsewhere are absent. On the other hand, the New Zealand land-snail fauna is highly diverse at genus and species levels. Spectacular diversification has occurred in the typically Gondwanan families Pupinidae, Rhytididae, Athoracophoridae, Punctidae, and Charopidae and the fauna is among the most speciose in the world for the land area. More than 99% of New Zealand's native land gastropods are endemic. The majority of species are forest-floor detritivores. Some are

arboreal, and graze mainly on phylloplane microorganisms. Others are carnivores, feeding on earthworms, amphipods, and other snails. A notable feature is the absence of herbivores of green plant tissues. Habitat fragmentation threatens the ecological integrity and genetic diversity of the native fauna, while some of the 31 species of introduced snails and slugs are serious economic pests.

Native terrestrial Deuterostomia comprise only vertebrate chordates – mostly birds, a moderately diverse herpetofauna, and two mammal species (Table 4). Of the four living species of leiopelmatid frogs, all are terrestrial but *Leiopelma hochstetteri* occurs alongside forest creeks, in seepages or in damp catchments above forest creek habitats (King et al. 2009). The Leiopelmatidae is an archaic family that includes only two living genera, including *Ascaphus* in North America. Primitive anatomical features include ‘tail-wagging’ muscles in the adult, retention of free ribs not fused to the vertebrae, and certain vertebral characters. The Leiopelmatidae may be the basal living frog family, related to Jurassic antecedents. The reptilian order Sphenodontia is likewise archaic and its presence in New Zealand today strongly supports a vicariant Gondwanan origin for the tuatara, which comprises two species and one undescribed subspecies. Apart from one introduced Australian species, all other terrestrial reptiles are lizards, comprising diplodactylid geckoes and lygosomine skinks. Two recent major phylogenetic studies have clarified the status of the New Zealand lizard genera in New Zealand. Whereas the two previous scincid genera *Cyclodina* and *Oligosoma* have been merged into the latter genus (endemic to Zealandia including Lord Howe and Norfolk islands) (Chapple et al. 2009), five new genera have been segregated from the gecko genus *Hoplodactylus* (Nielsen et al. 2011). Along with *Naultinus* (green geckoes), all native lizards are endemic. The continuing rapid rate of discovery suggests that the endemic herpetofauna could be as high as 100 species. Prior to the introduction of exotic mammals in New Zealand, reptiles would have been an ecologically important component in many habitats. Even today, where protection is afforded, densities of 140 individuals per square metre are known.

The terrestrial avifauna is not diverse by world standards (no genus contains more than seven species and few have more than five) but is taxonomically and ecologically distinctive. It is composite in nature, having an ancestry mixed in space and time. Approximately 245 species were breeding in New Zealand at the time of first human contact (estimated from Holocene fossils and the extant fauna) but this figure is dependent on opinion about subspecies/species status and the inclusion of recent colonists and vagrants. Trewick and Gibb (2010) review each of the orders, pointing out distinctive elements and temporal and geographic genetic relatedness to other areas or taxa. Iconic kiwi (Apterygiformes) and the recently extinct moa (Dinornithiformes) are classified either in their own orders (e.g. Bunce et al. 2009; Allentoft and Rawlence 2012; Worthy and Scofield 2012) or with all other ratites in Struthioniformes (Trewick and Gibb 2010). Including recently extinct populations, kiwi (*Apteryx*) comprise five allopatric lineages in a single family (Trewick and Gibb 2010). Worthy and Scofield (2012) recognise three families, six genera and nine species of moa. New Zealand has three endemic living species of parrots (Psittaciformes) – monotypic *Strigops habroptilus* (kākāpō) and two species of *Nestor* (kea, kākā). Strikingly, *Strigops*, *Nestor*, and Miocene *Nelepsittacus* (Worthy et al. 2011) appear to form a clade (superfamily Strigopoidea) that is sister to all other extant parrots (de Kloet and de Kloet 2005).

A third species of *Nestor* is recently extinct on Norfolk Island so Strigopoidea is functionally endemic to New Zealand. The radiation of the parakeet genus *Cyanorhamphus* (Psittacoidea) has produced six species, distributed on the mainland and subantarctic islands. The greatest land-bird diversity in New Zealand is found among the Passeriformes (song birds), in which there are three endemic families – Acanthisittidae (New Zealand wrens, five genera (three recently extinct), and seven species (five recently extinct, the sole survivors being the rifleman and rock wren)); Callaeidae (wattled crows, three genera (including huia, *Heterolocha*, recently extinct) and three living species); and Notiomystidae (stitchbird, one monotypic genus). Interestingly, like the Strigopidae in the Psittaciformes, Acanthisittidae have been found to form the sister taxon with all other songbirds (Ericson et al. 2002). *Mohoua* (yellowhead, whitehead) is endemic in the Pachycephalidae (whistlers and allies) and *Anthornis* (bellbird) and *Prosthemadera* (tūī) among the Meliphagidae (honeyeaters). The two species of recently extinct New Zealand thrushes (*Turnagra*) have been placed in their own family but a recent analysis concludes that *Turnagra* is an extinct oriole clade (Oriolidae) that diversified in New Zealand from a Miocene dispersal event from Australia (Johansson et al. 2011).

King et al. (2009) have thoroughly reviewed the status and diversity of the mammalian fauna of New Zealand, including introduced taxa reviewed elsewhere in this volume. The native terrestrial fauna comprises only two extant species of bats (Chiroptera); a third is recently extinct. The short-tailed bat, *Mystacina tuberculata*, is endemic at the family level (Mystacinidae); the long-tailed bat, *Chalinolobus tuberculatus* (Vespertilionidae), is endemic at the species level. *Mystacina* is an important seasonal pollinator of New Zealand's only fully parasitic native flowering plant, *Dactylanthus taylori*. The chances of the future survival of both highly-threatened species are linked.

#### Freshwater fauna

The freshwater environment is the least species-rich of the major environments in New Zealand, with only ~6% of all known animal species (Table 2).

Approximately 850 species of Hexapoda are found in New Zealand's fresh waters, all as larval stages, and some as adults, in 11 insect orders. Diversity is highest in Diptera (flies, 268 species), followed by Trichoptera (caddis, 249), Plecoptera (stoneflies, 120), Coleoptera (beetles, 83), Ephemeroptera (mayflies, 52), Odonata (dragonflies and damselflies, 15), Hemiptera (bugs, 10) and Neuroptera (lacewings, 5), with a single species each of Megaloptera (dobsonfly), Mecoptera (scorpionfly) and Lepidoptera (moth). Additionally, 47 species of lice (Phthiraptera) are associated with waterfowl hosts (Macfarlane et al. 2010).

Aquatic dipteran families are mainly in the suborder Nematocera, for example, Chironomidae (midges, 129 species), Tipulidae (crane flies, 63), Simuliidae (sandflies, 19), Blephariceridae (net-winged midges, 13), Culicidae (mosquitoes, 9), Dixidae (9), Tanyderidae (7) and Corethrellidae (1), but Brachycera also includes aquatic larval forms (e.g. Empididae (19) and Pelecorhyncidae (1)). These tallies pertain to endemic species. There are additionally two adventive freshwater mosquito species. At least 25 endemic freshwater genera are distributed among these families, the majority (18) in the Chironomidae. Several nuisance species are found among these taxa. Midges from the former Mangere oxidation ponds used to plague Aucklanders, and most New Zealanders will be familiar

with blood-feeding sandflies/blackflies and mosquitoes (two of them introduced species). New Zealand's stoneflies belong to four families that have a Gondwanan distribution. All species and 19 of the 20 genera are endemic. The presence of stoneflies is indicative of a healthy stream or river. The main beetle families of aquatic habitats are the Dytiscidae, Hydrophilidae, Elmidae, Hydraenidae and Limnichidae. Dytiscids (diving water beetles) are aquatic in larval and adult stages. New Zealand hydrophilids in ground water include some of the world's most primitive water beetles. Three genera each of Dytiscidae and Elmidae are endemic. All species and the 20 genera of Ephemeroptera are endemic, as are two apparently ancient families, Rallidentidae and Siphonaptera. Whereas larval mayflies may remain in flowing waters for up to 3 years, the non-feeding adults last little more than 48 hours at most. Larvae are food for invertebrates, fish and waterfowl; adults are food for insectivorous birds. The diversity of Odonata is relatively low, but three genera and 10 species are endemic. Nymphs and adults prey on smaller invertebrates while being preyed upon by waterfowl. Adults fall prey to spiders and robberflies, rats and birds. Aquatic Hemiptera belong to the suborder Heteroptera. Gerromorpha are semi-aquatic bugs that live on the water surface; Nepomorpha live beneath the surface. All five species of Corixidae (water boatmen) and the two species of Notonectidae (backswimmers), both Gerromorpha, are endemic. Only one freshwater species of Veliidae (Gerromorpha) is endemic. The low-diversity Neuroptera have 50% endemism. The sole species of Megaloptera, *Archicauliodes diversus*, the largest of all larval insects in running fresh waters, is endemic, but not the sole freshwater aquatic lepidopteran larva. Scorpionflies are an archaic group. The sole New Zealand species, *Nannochorista philpotti*, belongs to a family (Nannochoristidae) of just eight species that originated in the Late Permian, having a circum-Antarctic distribution. The family is distinct enough to have been separated as a separate suborder (Nannomecoptera) or even an order in a clade that includes Siphonaptera and Diptera (Beutel et al. 2009). Its phylogenetic position remains to be resolved.

Among arachnids, only mite species are found permanently submerged in fresh waters in New Zealand. There are 158 named species in 59 genera and 21 families and unnamed species of several other genera have been collected (Sirvid et al. 2010). All but one of the named species is endemic as are 35 of the genera. A further nine genera are strictly Gondwanan. Many of the taxa are very ancient, having originated in the Mesozoic.

Freshwater Crustacea are more diverse, comprising a fauna of 236 species – 41 Branchiopoda (water fleas and tadpole shrimps), 68 Maxillopoda (mostly copepods), 37 Ostracoda (seed shrimps), and 90 Malacostraca (mostly amphipods and isopods) (Webber et al. 2010). Endemism is low among the Branchiopoda, with no endemic genera and only five endemic species of Diplostraca. In lakes, calanoid copepods of the family Centropagidae (three endemic) dominate the zooplankton. The diversity of species is low but they are widely distributed and abundant. Higher diversities of cyclopoid (5 endemics) and harpacticoid (14 endemics) copepods are found on bottom sediments and submerged surfaces and in groundwater. Only *Abdiacyclops* is endemic among genera. Endemic *Paracyclops waiariki* (Cyclopoida) is the only known copepod of North Island geothermal waters, tolerating a pH of 3.1 and a seasonal temperature range of 29.5° to 37.5°C. By virtue of their numbers and size, copepods form a vital link in aquatic food webs, transferring energy from minute algal cells and protozoans to predators that ingest them. Some cyclopoid copepods are parasitic, infecting a variety of freshwater fish. Subclass

Ostracoda – mostly Cyprididae, Cypridopsidae, Darwinulidae, Limnocytheridae and Ilyocyprididae (Podocopida) – are widely disseminated in New Zealand fresh waters but remain poorly studied, especially the fauna of groundwater. Only the genus *Kiwicythere* (Limnocytheridae) is endemic. Food-mediated seasonal blooms in some freshwater habitats can temporarily result in vast numbers. Six orders of subclass Malacostraca are found in New Zealand fresh waters. The syncaridan orders Anaspidacea (six endemic species) and Bathynellacea (eight endemic species) comprise a group of freshwater crustaceans with a history extending back to the Carboniferous. While some are found in open water, the majority are inhabitants of subterranean groundwaters. Anaspidacea are found only in the Southern Hemisphere. All 4–6 species of the only family found in New Zealand (Stygocarididae) and the genus *Stygocarella* are endemic. Bathynellacea is more widely distributed globally. These very small crustaceans (0.4–3.5 millimetres) are represented in New Zealand by eight endemic species in two families. All have potential to be indicators of water quality. The peracaridan order Amphipoda is represented in New Zealand fresh waters by c. 54 species (~30 undescribed) in nine named (and at least 10 additional unnamed new) genera belonging to nine families. Amphipods are often surprisingly abundant, but have received little attention, probably because of small adult sizes (3–6 mm), although two hypogean species (*Phreatogammarus fragilis* and *Ringanui toonuiiti*) grow to over 20 millimetres. All New Zealand species, 5 named genera, c. 10 unnamed genera, and 3 families are endemic. Two species of groundwater Ingolfiellidea remain undescribed. The dominant hypogean freshwater members of Isopoda in New Zealand belong to suborder Phreatoicoidea (family Phreatoicoidea). Extant species have a Gondwanan distribution but the group was formerly cosmopolitan; Phreatoicoidea are the oldest isopod fossils and have not changed in 325 million years. All nine New Zealand species and three genera are endemic. The balance of eight freshwater native species belongs to suborders Cymothoidea (one monotypic endemic genus of Leptanthuridae), Sphaeromatidea (two endemic genera and four species of Sphaeromatidae) and Valvifera (three endemic species of Idoteidae). The mostly marine order Tanaidacea has one freshwater representative in New Zealand, the nearly cosmopolitan species *Sinelobus stanfordi*, which can be found in estuarine to fully freshwater habitats. In New Zealand it is known from freshwater sponges in lakes in the Rotorua district. Four freshwater Decapoda are found in New Zealand – a non-endemic crab (*Amarinus lacustris*, Hymenosomatidae), two crayfish (koura) species of the endemic genus *Paranephrops* (Parastacidae), and a monotypic endemic shrimp *Paratya curvirostris* (Atyidae). Koura are important taonga species for which there is some commercial aquaculture.

Freshwater nematodes have been little-studied in New Zealand. Yeates (2010) indicates just nine named species and additional unnamed parasites of freshwater fishes. Better known is the small fauna of horsehair worms (phylum Nematomorpha). Although there are only four freshwater species, they are a distinctive and significant group (Poinar 2010). In fact, owing to their numbers in the wild, New Zealand is one of the best countries in the world for studying hairworms, especially in the South Island. The free-living stages can occur in almost any type of fresh water, from sea level to high mountains. Three of the species are endemic and the fourth also occurs in South America. All native species have an indirect life cycle involving an aquatic paratenic host (a larval insect) and an adult developmental host

(an orthopteran, especially weta). The weta–hairworm relationship in New Zealand, involving different species of worm and host, is probably millions of years old and worthy of intensive study to resolve the still-unknown details.

The largest lophotrochozoan freshwater phylum in New Zealand is Gnathifera, with 484 species. These are mostly Rotifera, with 449 species, only 12 of which are endemic (Shiel et al. 2009); most are widely distributed or cosmopolitan. There are also seven endemic subspecies. Rotifer species richness in lakes is low compared to Northern Hemisphere lakes. Proportionately more species are associated with benthic substrata in lakes and as periphyton. The related parasitic thorny-headed worms (Acanthocephala) comprise six species having freshwater hosts.

Mollusca is represented by 89 freshwater species, chiefly freshwater snails of the family Hydrobiidae (Spencer et al. 2009, 2012), in which there are at least 64 described species (many more undescribed) in 14 genera (13 of them endemic). Endemic *Potamopyrgus antipodarum* is now one of the most successful invasive species abroad and is a local intermediate host for 14 species of Trematoda (flukes) whose adults live in fish, waterfowl, and mammals. Among the 18 species of freshwater pulmonates (many exotic) are two species of bioluminescent limpet in the endemic family Latiidae. There are two endemic species of hyriid freshwater bivalves, one in the endemic genus *Echyridella*, and three endemic sphaeriids.

The 78 freshwater species of Platyhelminthes are mostly flukes (42 species) and tapeworms (17 species) of freshwater primary hosts (e.g. fish) or of freshwater intermediate hosts (e.g. aquatic snails) that may infect terrestrial livestock (as in the case of the alien liver fluke that infects sheep, cattle and other mammals) (Johns et al. 2009). ‘Swimmer’s itch,’ a type of dermatitis reported from Lake Wanaka, is caused by one of several species of schistosomes (blood flukes). They infect waterfowl and it is the cercaria larvae that cause the ‘itch’ without actually being able to infect humans. There are also 16 species of ‘turbellarian’ (now rhabditophoran) flatworms, mostly triclads, of streams and subterranean waters, including *Temnohaswellia novaehelandiae* epizootic on freshwater crayfish (koura).

Among the less-diverse taxa in fresh waters are 55 species of Annelida, mostly Tubificida (Clitellata) of the families Phreodrilidae, Tubificidae, Naididae and Enchytraeidae (11 endemic species and many more introduced) (Glasby et al. 2009). There are nine species of leeches (six endemic). Freshwater Cnidaria are represented by five species of Hydrozoa (hydras and freshwater jellyfish), none endemic. There are eight species of freshwater Bryozoa, none endemic (Gordon et al. 2009) and five species (one endemic) in four genera of freshwater spongillid sponges (phylum Porifera) but their taxonomy needs revision (Kelly et al. 2009). At least five species of Nemertea (ribbon worms) occur in New Zealand, including monotypic endemic *Campbellonemertes johnsi* from Campbell Island. Two other species are endemic and two introduced (Gibson 2009). Phylum Gastrotricha is known to occur in New Zealand fresh waters but these have never been studied taxonomically.

Among deuterostomes, the freshwater fish fauna comprises 38 indigenous species and 20 exotic species (King et al. 2009; McDowall 2010, 2011). Galaxiidae (whitebait) is the largest native family, with 22 species (20 endemic), followed by Eleotriidae (bullies) with seven endemic wholly freshwater or diadromous species, Anguillidae (freshwater eels), with three species, one endemic, and Retropinnidae (including Prototroctidae, smelts and graylings), with two surviving endemic diadromous species, one

in the endemic genus *Stokellia*. There are three distinct elements in the fauna. First, the fauna is dominated by families whose relationships are with faunas in other southern cool-temperate lands, for example Geotriidae (lampreys), Retropinnidae and Galaxiidae. A second element in the fauna has relationships with other fishes in warmer subtropical seas to the north and west of New Zealand, namely the families Anguillidae, Eleotriidae, and Microdesmidae (dart gobies – if the last of these can be regarded as part of the freshwater fish fauna). The third element in the fauna comprises species derived from nearby coastal seas. This applies to the torrentfish *Cheimarrichthys fosteri* (Pinguipedidae), whose closest relative is believed to be the coastal blue cod (*Paraperca colias*). The habitats of many native species are threatened and studies of genetic diversity enhance the level of concern; *Galaxias vulgaris*, once regarded as a single widespread species, now comprises six species, some with highly restricted distributions.

New Zealand’s frog fauna includes one species of *Leiopelma* dependent on fresh water (see above). There are two naturalised Australian frogs in the genus *Litoria*. Including naturalised species, there are 35 species of waterfowl. These are all listed in King et al. (2009). The birdlife around lakes includes many species found in other wetlands such as swamps and estuaries. Among the more common extant native birds that are only found in or near ponds and lakes are grey ducks and grey teal and divers such as the scaup (all Anatidae), along with the New Zealand dabchick (North Island), crested grebe (South Island) (both Podicipedidae), and black-billed gull (Laridae). The larger birds are mostly introduced species, including mallard ducks, black swans (self- and human-introduced) and Canada geese (Anatidae). Anatiform birds were formerly more diverse in New Zealand, including at least eight recently extinct taxa. Wetland birds include shovelers and Paradise shelducks (Anatidae), coots, rails, crakes and pūkeko (Rallidae), different species of shag (Phalacrocoracidae), Australasian bittern (Ardeidae) and royal spoonbill (Threskiornithidae). Birds of wetland margins also include kingfisher (Alcedinidae) and fernbird (Sylviidae). Whio or blue duck (*Hymenolaimus malacorhynchos*) (Anatidae) is a distinctive endemic bird of fast rivers and streams, typically in forested areas, whereas black stilt (Recurvirostridae) is restricted to open braided river margins as well as streams and lakes in the Mackenzie Basin. A number of birds often associated with coastal wetlands can also be found inland, such as oystercatchers (Haematopodidae) and wrybill plover (Charadiidae).

#### Marine fauna

Marine species in New Zealand comprise almost 38% of the total known animal fauna. The four most speciose phyla in the marine environment, each with more than 1000 species, are Mollusca, Arthropoda, Chordata and Cnidaria (Table 2).

There are about 3600 marine molluscan species in New Zealand, including about 1200 in collections awaiting formal description (Spencer et al. 2009, 2012). The distribution of species among the seven classes is highly uneven but endemism in the EEZ is remarkably high overall (~85%) [endemism in brackets following species numbers]: Aplousobranchia 10 (100%), Polyplousobranchia (chitons) 64 (~85%), Monoplousobranchia 6 (100%), Bivalvia 637 (~85%), Scaphopoda (tusk shells) 47 (~98%), Gastropoda (sea snails/slugs) 2671 (~76%), Cephalopoda (octopus, squid) 123 (~23%). Some 182 marine genera are endemic. At class and subclass level, those groups with low levels of endemism are typically those with good dispersal powers, notably opisthobranchs and cephalopods. The overall high level

of endemism is concentrated in relatively few families in which almost all of the species are endemic, a pattern characteristic of faunas of remote island groups. These speciose groups comprise the marine gastropods Nacellidae, Trochoidea, Eatoniellidae, Rissoidae, Buccinidae, Columbelloidea, Muricidae, Marginellidae, Volutidae, and Conoidea, and the Octopodidae. This endemism can be explained by the fact that the species in these families have relatively limited dispersal ability. In contrast, marine families with multiple species that have distributions extending beyond the New Zealand EEZ, even those with long-lived planktonic larvae, show low endemism and/or low diversity within the EEZ; some families are lacking altogether. There has been an evolutionary shift into, and radiation of endemic taxa within, ecological niches dominated by other families elsewhere in the world. For example, species of *Cominella* (Buccinidae) are the predominant scavengers in New Zealand, whereas almost everywhere else this niche is filled by species of *Nassarius* (Nassariidae). Similarly, species of *Paphies* (Mesodesmatidae) are the dominant intertidal filter-feeding bivalves on open coasts in New Zealand, whereas elsewhere this niche is filled by species of *Donax* (Donacidae).

The uniqueness of the New Zealand Mollusca is exemplified by certain taxa that are outstanding from a biological and ecological perspective. Two species of large chitons from the New Zealand mainland stand out – *Cryptoconchus porosus* for its wholly internal shell plates, a character displayed by only one other species of chiton in the world; and *Pseudotonicia cuneata* for its life permanently within soft sediments. More than 8.5% of the world's chitons occur within the EEZ. New Zealand's largest mesodesmatid, *Paphies ventricosa* (toheroa), is one of the largest in its family worldwide. The patellid limpet *Patella (Scutellastra) kermadecensis*, which can reach 15 centimetres or more in length and is endemic to the Kermadec Islands, is the only living representative of its family in the EEZ. Among the Trochoidea one can single out the calliostomatids, several of which are larger than any others in the world, and the trochid *Diloma nigerrima*, which feeds on drift giant kelp amongst the breaking surf. The ostrichfoot snails, family Struthiolariidae, represent an infaunal, filter-feeding lineage of the superfamily Stromboidea. The nudibranch *Jason mirabilis* has an extremely large body size for an aeolid, yet its radula is so microscopic as to be nearly vestigial. The tiny, white, maggot-like slugs of the genus *Smeagol* live deeply buried in gravel above high-water mark. Some groups are notably diverse. For instance, there are far more living bivalves of the family Spheniopsidae (eight species) and glass-sponge-eating gastropods of the family Trochaclididae (13 species) than elsewhere in the world. New Zealand is also the world centre for speciation in gastropods of the genera *Pisinnia* (60 species and subspecies) and *Eatoniella* (42 species). Unusually high diversities are also shown in other marine Gastropoda – *Micrelenchus* (10 species), Calliostomatidae (39 species) and Buccinidae (87 species and subspecies).

A number of species are important food for Māori and/or the basis for commercial aquaculture. Seafood in 2012 was the seventh-largest export earner for New Zealand (the fourth in the edible category), of which the top-performing molluscs are green-lipped mussel, squid, oysters, and paua (abalone), which also produces mabé (hemispherical) pearls.

Arthropoda is the next most genetically diverse phylum in the New Zealand marine environment, comprising 2978 species, mostly Crustacea (Table 3). They range in genetic and morphological diversity from relatively lowly brine shrimp and cladocerans (class Branchiopoda), through armoured, sessile

barnacles (class Maxillopoda), pelagic open-ocean copepods and their benthopelagic and benthic relatives (also Maxillopoda), tiny bivalved planktonic and benthic Ostracoda, to highly organised, large mobile Malacostraca-like crabs and rock lobsters (order Decapoda) and their relatives in several other orders. There are also a number of parasitic forms, mostly in Maxillopoda (Webber et al. 2010).

Class Branchiopoda is represented by eight species of Cladocera in marine plankton and a species of brine shrimp in the hypersaline Lake Grassmere salt ponds. None is endemic. In contrast, the sole species of the rare subclass Cephalocarida, *Chiltonia elongata*, belongs to an endemic genus.

Class Maxillopoda is highly diverse, with more than 730 species dispersed among subclasses Thecostraca, Tantulocarida, and Copepoda. Thecostraca comprises a diverse group of shell-boring, parasitic, and filter-feeding forms generally all referred to in the past as barnacles. True barnacles (order Thoracica) comprise 83 acorn, wart and stalked-barnacle species of seashores, the open ocean, and the deep sea. Their ecological roles are significant, acorn barnacles comprising one of the major zone-forming organisms of seashores. Equally, they settle on ocean-going vessels and anthropogenic structures and have a major economic impact. Some 40 species and only a single genus (the predominantly chitinophosphatic (non-calcareous) iblomorph barnacle *Chitinolepas spiritsensis* from Spirits Bay) of Thecostraca are endemic. Tantulocarida comprises minute (>0.5 millimetres) ectoparasites of other crustaceans. There are three native species, two endemic. Copepoda is far and away the largest maxillopodan subclass, with at least 629 New Zealand species in six orders. Copepods are among the most numerous animals on earth owing to their predominance in marine plankton, where different species are characteristic of different water masses, but they are also abundant in bottom sediments and as associates of other animals. Fish-parasitic species, known as sea-lice, can be problematic in fin-fish aquaculture (but not yet in New Zealand). Few planktonic New Zealand species are endemic. Calanoids dominate in the plankton, harpacticoids and parasitic siphonostomatoids the benthos. The latter two orders have been partly studied but many New Zealand species remain to be described and many more will be discovered.

Class Ostracoda (seed shrimps) comprise more than 405 marine species. Podocopid and platycopid taxa from the shallow intertidal to the outer shelf have been the most intensively studied, being the most accessible. Only about six marine genera are endemic. Of particular interest are three living species of Punciidae with wide-open valves that resemble, in shape and ornamentation, some archaic taxa.

The marine species of class Malacostraca are distributed across 10 orders in New Zealand. Webber et al. (2010) list 1470 species but numerous recent works, especially Ah Yong (2010, 2012) and Gerken (2012) have increased this number to more than 1500 species. The most primitive order is Leptostraca (subclass Phyllocarida), with a history apparently dating from the Cambrian. The New Zealand fauna consists of five species in four of the 10 living genera. None is endemic. Order Stomatopoda (subclass Hoplocarida) comprises the mantis shrimps. Eight species (two endemic) in seven genera and five families are listed in Webber et al. (2010) but a recent monograph (Ah Yong 2012) has increased the number to 20 species (eight endemic) in 13 genera (two endemic) and 7 families. The remaining marine orders belong to subclass Eumalacostraca. The closely related orders Lophogastrida and Mysida respectively comprise 6 and 18

(11 endemic) species of opossum shrimps. There are no endemic genera. They are common in estuaries and coastal waters where they often congregate in large swarms and are important as food for fishes. Order Amphipoda has >415 marine species. Most are free-living and benthic; pelagic hyperiids live in the open ocean. Some amphipods are ectoparasitic on cetaceans and other organisms. The large numbers of amphipods in some biotopes render them important in food webs. Some 53% of New Zealand species and 19% of genera are endemic. Order Isopoda has ~340 marine species. Ecologically they comprise scavengers, herbivores, predators and parasites. Wood-boring species (gribble) can cause significant damage to pilings. Gondwanan affinities of the fauna are evident in the most speciose families, Sphaeromatidae and Cirolanidae. Endemism of New Zealand marine isopoda is high at the species level (c. 316 species or 77%); there are only eight endemic marine genera. Tanaidacea (tanaids) comprise at least 120 species (nearly half undetermined). An uncertain number of species (probably about two-thirds) and four genera are endemic. Cumacea (comma shrimps) comprise 75 species in Webber et al. (2010) but recent publications have increased this number to 89 (e.g. Gerken 2012). More than 66 species and seven genera are endemic. They live in surface sediments but after sunset can migrate into overlying water; swimming males are particularly prone to predation by fish. Order Euphausiacea (krill) has relatively low diversity but is very important ecologically, grazing on phytoplankton and small zooplankton and achieving high biomass that is important to cetaceans, seals, seabirds, and humans. All 19 New Zealand species are found elsewhere, in particular water masses or are bathypelagic. Decapoda is presently the most speciose malacostracan order in New Zealand, with almost 500 species (see also Yaldwyn and Webber 2011). It is the most important group economically insofar as it includes a number of edible commercial species (particularly rock lobster, scampi and paddle crab). The overall level of endemism is only ~30% at the species level. Ten genera and the family Belliidae are endemic. Endemism is lowest in pelagic offshore species and highest among benthic shallow-water forms.

Marine chordates are the next most diverse group in the EEZ, comprising ~14 500 species. The two major branches of craniates are the jawless fishes and the jawed vertebrates. It is still an open question whether hagfishes and lampreys have a common ancestor. They were once united in the Agnatha along with several fossil groups. Although hagfishes lack any kind of backbone, they do have a partial cranium (braincase) of cartilage. Lampreys, on the other hand, have some skeletal (cartilaginous) elements aligned along the notochord and flanking the spinal cord. To this extent they are vertebrates. Sequences of ribosomal and other genes give moderate to very strong support for a single clade containing hagfishes (class Myxini) and lampreys (class Cephalaspidomorpha). New Zealand's jawless-fish fauna is impressive. There are eight species in three genera (including endemic *Neomyxine*) and one, *Eptatretus goliath*, is the largest living jawless fish (Mincarone and Stewart 2006). By comparison, Australia has only five species in one genus and South Africa four species in two genera.

The largest single group of vertebrates in New Zealand is marine fishes, with a diversity of 1448 species that constitutes a globally unique mix of widespread (semi-cosmopolitan), Indo-Pacific, Australasian, sub-Antarctic and endemic taxa (King et al. 2009). Approximately half the species are widespread and about 19% are endemic. Currently, 148 species of cartilaginous fishes are known in New Zealand waters. Chondrichthyes is a diverse

group, comprising one order and three families of elephant fish and chimaeras, six orders and 18 families of sharks and dogfishes, and one order and five families of skates and rays. Some 27.4% are endemic. The most speciose families as currently classified are the kitefin sharks (Dalatiidae, 22 species), skates (Rajidae, 13), and catsharks (Scyliorhinidae, 11). The last two also have high levels of endemism. Families Narcinidae (slender electric rays) and Rajidae each include an endemic genus. New Zealand chondrichthyan fishes have many taxonomic problems that in some cases require regional or global revisions to resolve. More than 25% of the known fauna is unnamed or not presently determinable. About 90% of New Zealand's fishes are teleosts (1233 species), in 29 orders and 185 families, of which the most diverse group is Perciformes, followed by Gadiformes, Myctophiformes, and Stomiiformes. Among families, the pelagic lanternfishes (Myctophidae), benthic and benthopelagic rattails or grenadiers (Macrouridae), and pelagic dragonfishes (Stomiidae) are the most speciose. Families that give New Zealand its unique and most distinctive character include the coastal triplefins (Tripterygiidae), clingfishes (Gobiesocidae), right-eyed flounders (Pleuronectidae), and sleepers (Eleotridae). Families Congiopodidae (pigfishes), Psychrolutidae (toadfishes), Creediidae (tommyfishes), Eleotridae, Leptoscopidae (stargazers), Percophidae (opalfishes), Pinguipedidae (sandperches), Plesiopidae (rockfishes), and Uranoscopidae (armourhead stargazers) each include an endemic genus, Bithytidae (brotulas) and Clinidae (weed fishes) each have two endemic genera, Pleuronectidae has three, Gobiesocidae (with 13 species) has eight and Tripterygiidae (with 27 species) has nine.

New Zealand's marine-reptile fauna comprises seven non-breeding seasonal visitors – five turtles and two sea snakes. Out of a total bird fauna of 286 species, New Zealand has 122 species that may be classified as marine or maritime based on the criterion of spending all or almost all of their time feeding (affecting trophic and parasite/prey relationships) in those environments. Almost three-quarters of the world's penguin, albatross, and petrel species and half of shearwater and shag species occur or have occurred in the New Zealand EEZ (some Holocene extinctions). The coastal-feeding wrybill (*Anarhynchus frontalis*) is a monotypic endemic genus of Charadriidae (plovers). Six species of penguins still nest in the EEZ and one, *Megadyptes antipodes*, is a monotypic endemic genus. Seven of the 12 species of albatross (Diomedidae) that currently breed in the EEZ are endemic to the New Zealand region.

Among mammals, pinnipeds are important elements of New Zealand marine ecosystems. Three species are regularly seen on the mainland and subantarctic islands – the New Zealand fur seal *Arctocephalus forsteri* and, to a lesser extent and mainly in the south, the endemic New Zealand sea lion *Phocarctos hookeri* and the southern elephant seal *Merounga leonina*. Nearly half the world's cetaceans have been recorded in the EEZ, in other words, 43 species and subspecies. There are nine species of baleen whales, including the great whales (Balaenopteridae), such as the blue, fin, sei, Bryde's, minke, and humpback, plus the southern right whale (Balaenidae) and pygmy right whale (Neobalaenidae). There are 17 members of the dolphin family (Delphinidae), including two subspecies of endemic Hector's dolphin *Cephalorhynchus hectori*. Of the 17, 10 occur permanently and 5 are extralimital stragglers from tropical waters. There are 12 species of beaked whale (Ziphiidae). They are rarely seen at sea and are known mainly from stranded specimens. Three species of Physeteridae occur – sperm, pygmy sperm, and dwarf sperm whales.



Cnidaria (corals and anemones, jellyfish, hydroids) has 1113 marine species in the New Zealand EEZ, distributed among classes Anthozoa (octocorals, stony corals, black corals, anemones, 477 species), Hydrozoa (hydroids, hydrocorals, hydromedusae, siphonophores, 477), Scyphozoa ('true' jellyfish, 24), Staurozoa (stalked jellyfish, 5), and Cubozoa (box jellies, 1). Additionally, the Myxozoa, a class of microscopic parasites once known as Cnidosporidia and classified among Protozoa, is now recognised to constitute highly reduced cnidarians. There are 57 species in the EEZ (Cairns et al. 2009). Hydroids are the best-known group, thanks to recent monographs (Schuchert 1996; Vervoort and Watson 2003). The most speciose under-studied group is the Gorgonacea (Octocorallia), but new and ongoing studies since the 2009 review of the phylum (e.g. Cairns 2012) will remedy this situation. The phylum is well represented in the benthos and in rock-wall assemblages. In deeper water, especially on sea-mounts and rocky knolls, large, erect branching stony corals, black corals and gorgonians form significant habitat, enhancing local species diversity including fish populations for example, at some localities, commercial orange roughy. In pelagic waters, staurozoan jellyfish, smaller medusae and siphonophores constitute important predators of zooplankton and juvenile fish. A few species (notably cyaneid jellyfish and some siphonophores like Portuguese man-o-war) sting humans. Planktonic Cnidaria in benthic- and abyssopelagic realms have scarcely been sampled and their diversity remains largely unknown.

Bryozoa (bryozoans or moss animals), with 953 marine species in the EEZ (Gordon et al. 2009) and Porifera (sponges), with 742 species (Kelly et al. 2009; Reiswig and Kelly 2011), are two moderately diverse phyla with a sessile mode of existence. A number of the larger species of each group can also structure habitat in some biotopes much as corals can. More than 60% of New Zealand bryozoan species are endemic at the present day, as are 26 genera (with at least another 17 undescribed) and three families – the deep-sea Dhondtiscidae and Vinculariidae (the latter an Eocene 'hangover') and coastal Cinctiporidae. *Cinctipora elegans* is an important habitat associate of Bluff oyster in Foveaux Strait. Some 46% of sponge species are endemic but only about nine genera. New Zealand has globally high numbers of 'lithistid' (rock) sponges (including some 'living-fossil' taxa) and carnivorous sponges of the family Cladorhizidae (both class Demospongiae) and of glass sponges (class Hexactinellida). Many of the latter two groups remain undescribed but recent monography (e.g. Reiswig and Kelly 2011) is remedying the situation. Sponges (especially) and bryozoans are sources of marine natural products with applications to biotechnology and medicine (e.g. Blunt et al. 2013).

Phyla Annelida (segmented worms) and Echinodermata (sea stars and relatives) respectively have 800 (Glasby et al. 2009; Cutler 2009) and 633 (Mah et al. 2009; Anderson 2013) species in the EEZ. Most marine annelids are polychaetes (bristleworms, 767 species), with smaller numbers of clitellates including 11 leech associates of fishes. Polychaetes have a remarkable variety of morphologies and lifestyles and are important habitat-formers in some intertidal and subtidal biotopes, especially tubicolous species that form tubes of sediment grains or calcite. A few species are pelagic. Some are restricted to hot-vent or cold-seep chemosynthetic habitats and depend on their nutrition from endosymbiotic bacteria. Several tubicolous species are important marine foulers and these (and other species like *Sabella spallanzanii*) are alien invasives. About 45% of polychaete species are endemic, as are seven genera. Possibly seven of the marine-leech

species and three of the eight genera are endemic. Echiura (spoon worms – 7 species) are now recognised to be highly modified polychaetes and are included in Annelida. Echinodermata is exclusively marine. Species diversity is distributed among the classes as follows: Asterozoa (sea stars) 188 species, Ophiurozoa (brittle stars) 170, Echinozoa (sea urchins) 110, Holothurozoa (sea cucumbers) 101, Crinozoa (sea lilies and feather stars) 67. Some 237 echinoderm species (38%) and 18 genera are endemic. Among local species, the roe of kina (endemic *Evechinus chloroticus*) is used as food and the body wall of sea cucumber *Australostichopus mollis* has theoretical potential for a small sustainable fishery or aquaculture as bêche-de-mer.

Most marine Platyhelminthes (322 species) are fluke (199 species) and tapeworm (57 species) parasites of fishes, pinnipeds, cetaceans, seabirds and some invertebrates (Johns et al. 2009). There are also 64 species of 'turbellarians,' mostly polyclads and triclads. Trematoda has 71 endemic species and 11 endemic genera, Cestoda 8 endemic species and 2 endemic genera and 'Turbellaria' 11 endemic species and 1 monotypic endemic genus (*Okakarus ballantiniensis*). The known parasites of economic fishes have been listed by Diggle et al. (2002) but few have been investigated in detail as to their parasite burden and its effects. Tapeworms are important to the fishing industry because the larval stages occur in the flesh; hosts typically respond biochemically to kill the parasites, leaving unsightly discolorations in the flesh. The trematode *Bucephalus longicornutus* can occasionally infect Bluff oyster, and polyclad flatworms (as 'oyster leeches') can prey on commercial oysters, scallops, and mussels. At sea, larval trematodes have been known to cause mass mortality of a seabird (Claugher 1976). Ecologically, parasites in wild populations can manipulate their hosts to their advantage, thereby affecting ecosystem dynamics, as demonstrated in New Zealand estuaries where cockles can be affected by several species of flukes (e.g. Leung et al. 2010).

Tunicata, with 192 species, is often classified as a subphylum of Chordata. The majority of species are Ascidiacea (sea squirts and their colonial relatives, 168 species), which are benthic. The balance of species comprises planktonic Thaliacea (salps, 19 species) and Appendicularia (larvaceans, 5 species) (Kott et al. 2009). Certain species can be locally abundant and several are marine-fouling or invasive. Salps, while of low diversity, can sometimes bloom in such numbers as to temporarily dominate epipelagic zooplankton in summer, providing food, often when dead and fragmenting, to a variety of organisms, rapidly transporting primary production from the upper water layers to the seafloor, often in the form of faecal pellets. Appendicularians are similarly important, with potentially very fast growth rates, having the added ability to extract submicron particles from seawater. They are important food for fish and fish larvae.

Phylum Nematoda is possibly the most speciose animal phylum in the world's oceans according to some extrapolations based on deep-sea sampling, but the total number of described species in all environments globally is only about 27 000. In New Zealand, the total number of all known species is about 760 species and in the sea about 210, including parasites of fishes and other organisms (Leduc and Gwyther 2008; Yeates 2010). Marine free-living nematodes of New Zealand marine sediments are hugely under-studied – recent sampling of seafloor sediments on the Challenger Plateau and Chatham Rise to the west and east of New Zealand, respectively, have yielded more than 1200 species, at least 80% of which are undescribed (Leduc et al. 2012). Conservatively, several thousand additional species

remain to be discovered and described in all environments. The free-living marine species have an importance beyond their size. Their combined biomass in certain areas can exceed that of larger invertebrates. Further, they secrete copious amounts of mucous, by which they simultaneously bind sediment particles and also 'farm' bacteria, which they consume. They are also able to biosynthesise essential fatty acids, making them an important food source for larger animals (including juvenile or gill-raker-filtering fish) and can be used in fish aquaculture (Leduc 2012). At least 77 species of fish (mostly commercial) have been recorded as harbouring nematode parasites but none is a specific problem in fish aquaculture.

The balance of smaller phyla in the EEZ, with 50 species or less, add up to 277 additional taxa: Brachiopoda (lamp shells – 50 species), Kinorhyncha (mud dragons – 45 species), Gnathifera (including lesser jaw-worms, rotifers and thorny-headed worms – 44 species), Nemertea (ribbon worms – 29 species), Sipuncula (peanut worms – 26 species), Ctenophora (comb jellies – 19 species), Chaetognatha (arrow worms – 14 species), Kamptozoa (goblet worms, entoprocts – 12 species), Hemichordata (acorn worms and pterobranchs – 7 species), Dicyemida (worm-like parasites of octopod 'kidneys' – 6 species), Tardigrada (water bears – 5 species), Priapulida (penis worms – 4 species), Loricifera (corset worms – 4 species), Gastrotricha (meiofaunal worm-like organisms known only to genus in New Zealand – 4 species), Phoronida (horseshoe worms – 3 species), Xenacoelomorpha (mostly acoel flatworms, no longer classified among Platyhelminthes – 2 species), Cephalochordata (lancelets or amphioxus – 1 species), Nematomorpha (hairworms – 1 species), and Orthonectida (tiny parasites of invertebrates formerly classified, with Dicyemida, as Mesozoa – 1 species). Not all of these are named to species and many more taxa are expected for some groups, especially Nemertea, Gastrotricha, and Xenacoelomorpha. All of these phyla are reviewed by several authors and the known species listed in Gordon (2009, 2010). Of the 277 species, only 61 are endemic, mostly in Nemertea (21 species), which also includes nine endemic genera (Gibson 2009). Brachiopoda includes three endemic genera. These phyla, which cover a considerable range of high-level genetic diversity, are of zoological interest for the light they can shed on animal evolution.

In a review of New Zealand's marine biodiversity, Gordon et al. (2010) compared tallies for the EEZ with what is known in the best-studied area of the world, namely the region covered by the European Register of Marine Species (WoRMS), which, at 21.76 million square kilometres, is about 5.5 times larger than the New Zealand EEZ, but has only about twice as many species of Animalia. Interestingly, for each of the seven most intensively studied phyla in New Zealand (Cnidaria, Mollusca and Chordata relatively large, Bryozoa and Echinodermata medium-sized, Brachiopoda and Kinorhyncha small), the species tallies are comparable to those published for the entire ERMS region and in some cases (Brachiopoda, Bryozoa) exceed them. The comparison is uneven insofar as the New Zealand figures include known-undescribed species while ERMS does not, but the implication is that, when all animal phyla in New Zealand waters are as well studied, their total diversity may equal that in the very much larger ERMS region (in which the rate of discovery of new species is likely to be much less than for New Zealand). Further, if this equivalence holds more or less true for all animal phyla, then the figures for the ERMS region provide a useful proxy for the final species numbers that may be expected in the New Zealand EEZ, regardless of whether the taxon is large or small. Based on

the data to date, this equivalence invites testable hypotheses to explain it.

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