This ancient phylum of mostly marine organisms is best known for its contribution to geomorphological features, forming thousands of square kilometres of coral reefs in warm tropical waters. Their fossil remains contribute to some limestones. Cnidarians are also significant components of the plankton, where large medusae – popularly called jellyfish – and colonial forms like Portuguese man-of-war and stringy siphonophores prey on other organisms including small fish. Some of these species are justly feared by humans for their stings, which in some cases can be fatal. Certainly, most New Zealanders will have encountered cnidarians when rambling along beaches and fossicking in rock pools where sea anemones and diminutive bushy hydroids abound. In New Zealand’s fiords and in deeper water on seamounts, black corals and branching gorgonians can form veritable trees five metres high or more. In contrast, inland inhabitants of continental landmasses who have never, or rarely, seen an ocean or visited a seashore can hardly be impressed with the Cnidaria as a phylum – freshwater cnidarians are relatively few, restricted to tiny hydras, the branching hydroid \textit{Cordylophora}, and rare medusae.

Worldwide, there are about 10,000 described species, with perhaps half as many again undescribed. All cnidarians have nettle cells known as nematocysts (or cnidae – from the Greek, \textit{knide}, a nettle), extraordinarily complex structures that are effectively invaginated coiled tubes within a cell. When triggered, the cnidae are explosively evaginated, their barbed tips penetrating cells of other organisms and discharging toxins. Thousands of these are found in the tentacles of anemones, medusae, and hydroids, which are all effectively carnivorous, whether they capture large prey or suspension-feed on small particles. Some cnidarians employ mucus feeding in conjunction with nematocysts.

Cnidarians are diploblastic, having two cellular layers separated by a jelly-like mesogloea in which skeletal elements can occur. The inner cellular layer (endoderm or gastrodermis) lines the sac-like digestive cavity that lacks a separate anus; the outer cellular layer (ectoderm or epidermis) contains nematocyst-producing cells, cells of the nerve net, and epithelio-muscular cells. A distinctive feature of the phylum is the dimorphic body form into polyp and medusa, which probably accounts for the range of morphological and ecological diversification. (The word polyp, which means ‘many feet’, is derived from \textit{poulpe}, the French word for octopus, because an early French naturalist thought that cnidian tentacles resembled the arms of an octopus.) Among the five classes,
the Anthozoa (e.g., corals, anemones) have only the polyp phase, whereas many Scyphozoa (jellyfish) and Hydrozoa (hydroids) have both phases or one of them is lost. In the Staurozoa (stalked jellyfish) and Cubozoa (box jellies), the tiny polyp is transformed into the medusa. When both phases are present, in a kind of ‘alternation of generations’, gonads develop in the medusa. The fundamental symmetry of the Cnidaria was probably biradial (Marques & Collins 2004) but both polyp and medusa can be secondarily four-sided, or tetramerous. The ability of the polyp phase to bud asexually in many cnidarians allows them to form large colonies. In some taxa the polyps are differentiated into separate feeding, defensive, reproductive, and other forms—a phenomenon known as polymorphism, which is better developed in the Cnidaria than any other phylum. Evolutionary studies suggest that the Anthozoa is the most ‘primitive’ group and a sister to the rest of the Cnidaria (Schuchert 1993; Bridge et al. 1995), hence the medusa is derived.

A good starting place for general information on Cnidaria is www.ucihs.uci.edu/biochem/steele/default.html, which serves as a centralised web portal for all things cnidarian.

History of studies on New Zealand living cnidarian diversity

The earliest named New Zealand species of Cnidaria were mostly anthozoans—six species of scleractinian (stony) corals, anemones, and ‘dead men’s fingers’—described by Quoy and Gaimard (1834) from Astrolabe Expedition material. These were listed again by Gray (1843), who also described five species of thecate hydroids in his faunal review accompanying Ernst Dieffenbach’s Travels in New Zealand. A detailed history of the discovery of New Zealand Scleractinia was given by Cairns (1995), who noted the important contribution of expeditions in the development of knowledge of New Zealand’s marine biodiversity—in chronological order, the Astrolabe (1837–40), Challenger (1873–76), Gazelle (1874–76), Terra Nova (1910–13), Dana (1928–30), and Discovery II (1931–33), prior to the modern period of oceanographic exploration around New Zealand from the 1950s onward. Thus, most of the records of Cnidaria in Hutton’s (1904) listing of all known species in the Index Faunae Novae Zelandiae were based on nineteenth-century expedition reports and Hutton’s own research as New Zealand’s foremost natural historian. Significant early records subsequent to Gray (1843) included: Actiniaria (sea anemones) (Coughtry 1875a; Hutton 1879, 1880; Farquhar 1898), Scleractinia and Stylasteridae (Duncan 1876; Moseley 1881), Antipatharia (black corals) (Brook 1889), Octocorallia (gorgonians, sea pens) (Kölliker 1880; Wright & Studer 1889; Dendy 1897), Hydroidea (Hutton 1873, Coughtry 1875b, 1876a, b; Thompson 1879; Farquhar 1895, 1896; Hilgendorf 1898; Dendy 1902), Siphonophora (Haeckel 1888), and Scyphozoa (von Lendenfeld 1884a, b, c). Hutton’s (1904) non-critical Cnidaria list included 136 species (Anthozoa 37 species, Scyphozoa six species, Hydrozoa 99 species). This review of cnidarian diversity around the turn of the last century provided a useful basis for future studies.

Subsequently, Dennant (1906) and Benham (1907, 1909, 1928) added new records and species of anthozoans and medusae, Stuckey (1909a, b, c, 1914), Kirk and Stuckey (1909), and Carlgren (1924) described some Actiniaria, and Hilgendorf (1910, 1911), Hickson (1912), Bale (1924), Finlay (1928), Totton (1930), and Broch (1942) continued studies on New Zealand hydroids (including Stylasteridae). Vaughan (1917) was the first to report zooxanthellate corals from New Zealand, recording six Recent species and four fossil species from the Kermadec Islands. Totton (1923) described New Zealand antipatharians, Kramp (1928) added hydromedusae, Gardiner (1929) scleractinians, and Stiasny (1940) some Scyphozoa. The period following the Second World War saw a flurry of systematic activity on many phyla in the New Zealand biota, especially by New Zealand-born or -trained taxonomists. Inter alia, Brewin (1945) described New
Zealand stoloniferan octocorals and Parry (1951, 1952) thoroughly reviewed the Actiniaria, describing several new species – this latter work was continued by Ottaway (1975a,b), who clarified the status of several of the species dealt with by Parry. But the most influential post-war New Zealand contributor to an appreciation of cnidarian (especially hydrozoan) diversity was Patricia Ralph of Victoria University of Wellington. In a series of papers (Ralph 1947, 1948, 1953, 1957, 1958, 1961a,b,c,d; Ralph & Squires 1962; Squires & Ralph 1965) she described a range of cnidarians, including a hydromedusa, stylasterids, antipatharians, and especially thecate and athecate hydroids.

Increasing academic contacts between New Zealand marine biologists and overseas institutions ensured significant extra-New Zealand input to describing the biota where indigenous specialists were lacking. Inter alia, Carlgren (1954), Cutress (1961), and Hand (1961a, 1976) added to the actinian fauna, Squires (1960a, 1963, 1964a,b) clarified the scleractinian fauna, and Boschma (1966, 1968a,b,c,d) added to knowledge of the stylasterid fauna. Although it deals with only Monomyces rubrum, Squires’ (1963) monograph of this species is a classic, including an extensive synonymy, description, and ecological remarks of this variable and common coral.

In 1954, the New Zealand Oceanographic Institute (NZOI) was established as a new division of the then Department of Scientific and Industrial Research (DSIR). This made possible a programme of systematic sampling of New Zealand shelf benthos. Taxonomic work on the growing NZOI biology collection began to be published in the series New Zealand Oceanographic Institute Memoirs, which, since NZOI was subsumed in the National Institute of Water & Atmospheric

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### Summary of New Zealand cnidarian diversity

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Marine</th>
<th>Freshwater</th>
<th>Fossil*</th>
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</thead>
<tbody>
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</tr>
<tr>
<td>Staurozoa</td>
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<td><strong>Totals</strong></td>
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<td>14</td>
<td>204</td>
</tr>
</tbody>
</table>

* Includes about 19 species still living.
Research (NIWA) in 1992, continues as NIWA Biodiversity Memoirs. A number of major monographs of a range of cnidarian taxa have been published in recent decades, reviewing all previous taxonomic work and significantly increasing the number of known species. In chronological order, the taxa include Scleractinia (Squires & Keyes 1967; Cairns 1995), isidid Gorgonacea (Grant 1976), Stylasteridae (Cairns 1991), athecate hydroids (Schuchert 1996), hydromedusae (Bouillon & Barnett 1999), and thecate hydroids (Vervoort & Watson 2003). Monography is under way on the Actiniaria, Octocorallia, and Antipatharia for publication as NIWA Biodiversity Memoirs. Based on all published and unpublished literature and knowledge of species in collections, including the Myxozoa, the living New Zealand cnidarian fauna stands at 1,126 species, of which 330 are still unidentified and/or undescribed. There are also 204 fossil species.

Class Anthozoa – corals, anemones, and kin

Anthozoans comprise the largest group of Cnidaria, with about 6,000 living species worldwide. All are marine and there is no medusa phase. The mouth opens into a stomach cavity that is partitioned by mesenteries that expand the inner absorptive surface. There are two subclasses – the Octocorallia (Alcyonaria), which have eight mesenteries and tentacles, and the Hexacorallia (Zoantharia) with tentacles and mesenteries in multiples of six.

Subclass Octocorallia

This subclass used to be divided into a number of orders, all but one colonial, in which the polyps are united by stoloniferous cords or sheets of tissue (coenenchyme). The eight tentacles of the polyp are distinctively pinnate. Skeletal elements are variably developed and may comprise sparse to abundant calcareous (calcite) sclerites scattered throughout the colonial mesogloea or, in the case of many gorgonians, their axes may be constructed of scleroprotein and extremely rigid. Recent molecular results suggest that a new classification at ordinal and subordinal levels is necessary owing to the presence of both paraphyletic and polyphyletic groups in the current classification (Sánchez et al. 2003). In the New Zealand EEZ, 243 octocoral species (185 undescribed) are known, divided among 96 genera in 28 families. These include 45 species of Alcyonacea (stoloniferous and soft octocorals), 167 species of Gorgonacea (gorgonians), and 31 species of sea pens. Octocorals are rare intertidally though an inconspicuous species of Clavularia is quite common on rocky shores. Dead men’s fingers, a species of Alcyonium, is frequently encountered in shallow water. New Zealand soft corals do not achieve the size or diversity of those in tropical settings such as the Great Barrier Reef, nor are fan corals (gorgonians) as prominent as in the Atlantic, although some species attain a metre high at diveable depths off northeastern parts of the North Island. The diversity of three families of deep-water calcified gorgonians (Isididae, Primnoidae, and Chrysothectidae) is probably the highest in the world for a single country, however. Some primnoids can be observed at scuba depths, which is the shallowest record for this group, along the northeast coast of the North Island and at offshore islands from the Three Kings to the Poor Knights. Sea pens are generally found at shelf depths, but one species, Pteroeides bollonsi, is also encountered by divers in Fiordland.

Large gorgonians appear to be ecologically significant on seamounts, knolls, and hills in the New Zealand Exclusive Economic Zone. The stature of their colonies is made possible by the enhanced development of skeletal material. In holaxonians the axis is horny or woodlike, owing to the presence of a scleroprotein called gorgonin, and may be further strengthened by impregnation of calcium carbonate, but there are no sclerites in the axis. In bamboo corals (family
Isididae) the axis is conspicuously jointed, with solid calcium carbonate between the joints. In isidids as well as other calcaxonians (highly calcified gorgonians) such as Primnoidae and Chrysogorgiidae, it is observed in cross section that the axes may give evidence of distinct growth rings. These calcified groups may act as ‘reef-building corals’ in deep waters. In scleraxonians, a polyphyletic nominal group, their branching structure is composed of sclerites, and growth rings are not evident. All groups contain species that may become very old and robust, providing nursery habitat for a myriad invertebrates and fish.

Owing to the inadequate state of knowledge of species-level taxonomy, it is not possible to evaluate the degree of endemism of the New Zealand octocoral fauna, but there are some interesting features. *Taiaroa* is not only an endemic genus but its sole species is, unusually, solitary, comprising a single polyp, a character that at one time was regarded as typifying an order Protoalcyonaria (Bayer & Muzik 1976). New distributional records include two sea pen genera – *Acanthoptilum* and *Stylatula* – previously known only from North and South America. The bubblegum corals (Paragorgiidae) have a centre of endemism in New Zealand waters, with nine (eight endemic) of the 17 species in the family found in the EEZ (Sánchez 2005). There are many undescribed species of calcaxonians that could be endemic to New Zealand, and very rare groups of other gorgonian corals (e.g. *Anthomastus robustus* (Alcyoniidae) and the family Ifalukelidae) have been discovered on New Zealand seamounts, which may harbour one of the most diverse and unique octocoral faunas in the world.

**Subclass Hexacorallia**

Hexacorals may be solitary or colonial, soft or hard, the latter having rigid calcified skeletons. Soft hexacorals comprise the orders Ceriantharia (tube anemones), Actiniaria (sea anemones), Corallimorpharia (coral-like anemones), and Zoanthidea (zoanthid anemones). Hard hexacorals comprise the orders Scleractinia (stony corals) and Antipatharia (black corals). In the stony (or true) corals, a rigid septum is secreted between pairs of mesenteries. The septa remain in the dead coral skeletons. Recent molecular work indicates that the tube anemones comprise a sister taxon to the remaining orders (France et al. 1996; Daly et al. 2003).

**Order Ceriantharia**

Tube anemones are solitary tube-dwelling hexacorals living in muddy bottoms. They are not a diverse group and the two New Zealand species have not been identified to species. Even less is understood about their ecology. A larval cerianthid (known as *Arachnanthus*) has been found in the plankton in central New Zealand that is probably conspecific with one of the adult forms.

**Order Actiniaria**

Sea anemones are well known to New Zealanders. Children fossicking in rock pools enjoy probing anemone stomach cavities to feel the gentle tug of the cnidae, the toxins benign enough not to be felt as a sting. People familiar enough with New Zealand seashore animals to be able to recognise five or six common sea anemones may be surprised to learn that the actinian fauna is fairly diverse. A list compiled from the literature by Dawson (1992) contained 64 species. This number was increased when, in 1996, one of the authors (O. Ocaña V.) travelled around New Zealand collecting, photographing, and preserving actinians and other soft hexacorals. A new list based on these field collections, museum material, and a reconsideration of the literature contains 111 species, of which 92 are sea anemones. Since 1996, Ocaña has been studying the New Zealand collections in detail, a time-intensive task requiring thin-sectioning of paraffin-embedded specimens or tissues to determine the key anatomical characters, including the arrangement of mesenteries and the variety of cnidae.
The results of the study to date are indicated by the range of families, genera, and species in the Actiniaria checklist below.

Why does New Zealand have such a high diversity of soft hexacorals, especially actinians? The number of soft-hexacoral species currently recognised exceeds or even doubles that in some other regions, such as the Mediterranean, northeastern Atlantic, northwestern Atlantic, Caribbean, and central Macaronesia (Canary Islands and Madeira). Contributing factors may include the wide latitudinal range, from nearly subtropical (Kermadec Islands) to cool subantarctic (Campbell Plateau), and the large variety of marine habitats. New Zealand’s long history of geological isolation has also provided opportunities for speciation but, until the study is complete, it is not possible to comment in detail on endemism. On the other hand, the fauna includes species with wide distributions. Generally, actinian larvae disperse passively by ocean currents and shipping. The latter may explain the distribution of some environmentally tolerant species such as cosmopolitan *Haliplanella lineata* found in ports and harbours. It is difficult to speculate on the origin and diversity of any actinian faunas because of the lack of a fossil record, but if supposed centres of diversity are characterised by high species richness, then New Zealand may be one. So, either New Zealand is a speciation centre or, more plausibly, part of one that included the adjacent lands of former Gondwana. The present Gondwana-wide distribution of *Bolocera kerguelensis*, *Condylanthus magellanicus*, *Helianthella spp.*, *Paranthopsis cruentata*, and *Phellia aucklandica* supports the latter idea (Ocaña 1997).

There are some novelties in the New Zealand actinian fauna. One of the more remarkable is *Cricophorus nutrix*. Its young develop attached to the external surface of the parent, a phenomenon known as external brooding. Few species of sea anemones anywhere in the world are external brooders. Most belong to the genus *Epiactis*. But the New Zealand species of *Epiactis* do not brood externally, and *C. nutrix* belongs to a group of anemones only very distantly related to *Epiactis*. Indeed, *C. nutrix* may be unique among its relatives in this reproductive attribute. While *C. nutrix* is widespread in New Zealand and inhabits shallow water, it is rarely seen because it is the same colour as the weed to which it commonly attaches. Another cryptic shallow-water New Zealand anemone is the appropriately named *Mimetridium cryptum*. It occurs most commonly in places not exposed to sunlight, having been found in shipwrecks. It mimics northern hemisphere *Metridium senile*, which is used in many textbooks to illustrate a ‘typical anemone’, and that is the source of its genus name, but it is not closely related to *Metridium*, illustrating well how external morphology can be misleading in understanding phylogeny of anemones, and even taxonomy. In many parts of the world, some sea anemones live on gastropod shells occupied by hermit crabs. New Zealand has two such species, *Calliactis conchicola* and *Paracalliactis rosea*; remarkably, both may occupy a single snail shell. New Zealand also has two species of the little-seen ring sea anemones, which clasp a gorgonian branch by completely encircling it (Ocaña et al. 2004).

**Order Zoanthidea**

Twelve species are listed in the checklist at the end of this chapter. Their taxonomy is poorly known and awaits monographic work. Almost nothing is known about their biology other than the association of several species with sponges, hydroids, and molluscs. A striking yellow species of *Parazoanthus* is frequently encountered on Fiordland black coral. There is also a new species of Gerardiidae from New Zealand – a family able to generate its own skeleton.

**Order Antipatharia**

Until recently, the number of black coral species known in New Zealand waters was only 10. An ongoing study, since 1999, of New Zealand material has increased the fauna to 66 species, representing about 41% of the approximately 160 species now known from the entire Indo-Pacific. This unexpected diversity...
was discovered in the NIWA biology collection in Wellington. Additional specimens of many of the species also occurred in the Museum of New Zealand Te Papa Tongarewa.

Black corals are distinguished by their erect, often bushy, habit of growth and hard proteinaceous skeleton that bears tiny polyps. The skeleton may be naturally lustrous, or rendered so after polishing, and some overseas species are harvested to make into jewellery. None of the New Zealand species has been found to be suitable for this purpose, and, in any case, all native species are strictly protected. Although the depth and geographic distribution of the Antipatharia have not yet been analysed in detail, it appears that most species live in the deep sea and on seamounts between 200 and 1,000 metres depth. Several very rare species were discovered in the NIWA collection, including only the second known specimen of *Saropathes scoparia* originally collected from the Three Kings Islands in 1910 by the British *Terra Nova* Expedition (Opresko 2003). The collection also contained numerous specimens of *Cladopathes plumosa*, previously also known from only a single specimen. Of the 66 species found, eight to 10 appear to be new and undescribed, adding to the number of endemic black coral species in New Zealand waters. Additional study is needed to determine if other undescribed species are present in the NIWA collection.

**Order Corallimorpharia**

Four species are known in the New Zealand EEZ. The commonest is the variable jewel anemone, *Corynactis australis* (which may be more than one species), found in low-tidal rock pools and shallow diveable depths. The species looks like a spreading colonial sea anemone. Each tentacle is tipped with a characteristic knob (acrosphere) that is densely and minutely studded with cnidae.

**Order Scleractinia**

Stony corals are often regarded as characteristic, even diagnostic, of the tropics, and so it may be thought remarkable that New Zealand, not a tropical country, has a diverse fauna of 129 species. But it must be understood that not all stony corals contain in their tissues the symbiotic dinoflagellates (kingdom Protozoa) known as zooxanthellae that are characteristic of reef corals. In fact, of the 1,314 valid living species of Scleractinia (Cairns 1999a), fully 669 species (51%) lack these algal symbionts and, as a result, can be found in a range of water temperatures (−1°C to 29°C), from the Norwegian Sea to Antarctica and from the intertidal to 6,328 metres depth (Cairns 1982; Zibrowius 1980). These predominate in the New Zealand region. Zooxanthellate corals, by contrast, are restricted to warm tropical waters and to depths no greater than about 100 metres (Fricke & Schuhmacher 1983). The figure of 129 species for the EEZ culminates 177 years of research on New Zealand Recent Scleractinia. Cairns’s (1995) monograph described 21 new species and listed 71 new records, resulting in a total of 105 azooxanthellate species from the New Zealand region. Although only five years have passed since that publication, the number of azooxanthellates is herein reported as 112, an increase of seven species. This has resulted from adding eight more species (Cairns & Zibrowius 1997; Cairns 1999b; Brook 1999) and deleting five species because they occur outside the New Zealand EEZ in Australian territorial waters (Lord Howe, Norfolk, and Macquarie Islands) (see also Cairns 2004).

Only 17 zooxanthellates are known from the New Zealand EEZ, all from the Kermadec Islands, where they are near the southern limit for hermatypic and do not form actual reefs. Schiel et al. (1986) and Kosmynin (1994) are the first to have reported new material since Vaughan (1917), increasing the zooxanthellate list to 13 species. The 17 species recorded by Brook (1999), corrected for synonymy, constitute only 2.6% of the 656 known zooxanthellate species. The 129 scleractinian species comprise 9.7% of the total worldwide scleractinian species diversity of 1,314. Most of the New Zealand species...
are azooxanthellate, comprising 16.4% of the 669 known azooxanthellate species. Azooxanthellates are sometimes called ‘deep-water corals’ or ‘solitary corals’ although, in fact, some occur in shallow water and some are colonial; for example, in New Zealand waters, 17% of the azooxanthellates are colonial and 14 species can be accessed by scuba. Thus, although azooxanthellates are usually smaller, more slowly growing, and non-reef-forming compared with their zooxanthellate reef counterparts, as a group they are more environmentally tolerant and thus much more widely distributed.

All corals begin life attached to a substratum, but many subsequently become free by detaching from the substratum or overgrowing it, some even adopting an interstitial habit. Free-living species are commonest among the solitary deep-water fauna. All corals possess an aragonitic calcium carbonate skeleton (a corallum) that is usually white, although in some species may be mottled or streaked with brown, black, or even pink pigment. The corallum varies considerably in size. The smallest New Zealand species, solitary Conocyathus zelandiae, has a maximum diameter of about 3.5 millimetres and height of six millimetres, whereas the colonial framework builder Goniocorella dumosa may produce colonies over a metre in height. The corallum consists of a wall (theca) that may be granular or porcellanous in texture and often bears longitudinal ridges (costae). The round to elliptical oral surface of a solitary corallum is the calice. In most corals, the calice is regularly and hexamerally subdivided by calcareous radial partitions (septa), each supporting a pair of soft mesenteries. Usually there are 24, 48, or 96 or more septa per calice. Small accessory lobes (pali or paliform lobes) are sometimes present on the inner edges of certain septa. Directly in the centre of the calice is the columella, which may take the form of a lamella, a spongy mass, a single rod, a field of simple or twisted rods, or simply a indistinct fusion of the inner edges of the larger septa. Higher-level classification of scleractinian corals is based on the microstructure of walls and septa, whereas genus- and species-level distinctions are based on differences in corallum shape and attachment, costal architecture, presence or absence and number of pali and paliform lobes, the number, arrangement of shape of the septa, and characteristics of the columella (Cairns 1981).

The percentage of species considered to be endemic to New Zealand has decreased over the years as the fauna has become better known and comparisons

![A generalised solitary coral.](image)
have been made worldwide. Vaughan and Wells (1943) cited 56% endemism, Squires and Keyes (1967) 48%, and Cairns (1995) 31%. When New Zealand is strictly defined by its EEZ, however (not including Norfolk or Lord Howe Islands as in Cairns (1995)), the level of endemism drops to 19% (21 species) (see also Cairns 2004). It is interesting to note that some species once considered to be endemic to the western Atlantic are now being found in the South Pacific, such as *Tethocyathus cylindraceus*, *Stephanocyathus coronatus*, and *Dasmosmilia lymani*, as well as a subspecies of an Atlantic species, *Fungiacyathus pusillus pacificus*.

By far the commonest zoogeographic affinity (81 species, 74%) of the New Zealand azooxanthellates, however, comprises those species that are widespread in the tropical region of the Indo-West Pacific but have their southern boundary at varying degrees within the New Zealand region. For instance, 50 of these 81 species have their southern limit in the subtropical Kermadec Islands; 13 ‘eurythermic tropical’ species (Briggs 1974) extend into the warm-temperate Auckland province; nine species extend into the cool-temperate region of New Zealand (‘broad eurythermic tropical’); and another nine species extend into the subantarctic region of New Zealand. Another seven of the 112 azooxanthellate species (6%) are restricted to the temperate region, five are restricted to the southern temperate regions, and two species have disjunct distributions including northern temperate and southern temperate regions. *Hoplangia durotrix*, a shallow-water species known from the Mediterranean and northeastern Atlantic as well as North Island, New Zealand, is included in the last category. Cairns (1995) considered this to be adventive. *Flabellum impensum* is considered to be a subantarctic species with a northern range in the cool-temperate region of New Zealand.

The percentages cited above are based on the zoogeographic analysis of Cairns (1995), recalculated in light of later taxonomic revisions (i.e. Cairns & Zibrowius 1997; Cairns 1997, 1998, 1999a), which had the effect of reducing the number of endemic species and broadening the ranges of other species.

Bathymetrically, New Zealand azooxanthellates range from the intertidal to 4,954 metres depth; however, most (80%) occur at upper-slope depths of 200–1,000 metres. About 40 species occur at shelf depths (0–200 metres); 14 of these are accessible by scuba. Six species have abnormally shallow occurrences in the cold, upwelled waters of Fiordland. Cairns (1995) found a faunistic break among the azooxanthellates at 100 metres and at 400 metres.

The biogeography of the 17 zooxanthellate species at the Kermadec Islands was reviewed by Brook (1999). No zooxanthellate species is endemic to the Kermadecs; in fact, all but one (*Hydnophora pilosa*) also occur on the Great Barrier Reef. The basic affinity of the Kermadec zooxanthellates is the same as that of the majority of azooxanthellates – a depauperate fauna consisting of species having at the Kermadecs the southern boundary of a more widespread Indo-West Pacific distribution.

**Class Scyphozoa – jellyfish**

The Scyphozoa is a small group of cnidarians comprising only about 250 living species. Notwithstanding the low species diversity, this minor group has caused some major problems recently around the world and in New Zealand. Understanding of jellyfish-bloom dynamics remains incomplete, but large financial losses resulting from jellyfish invasions continue to be reported. Examples include the clogging of intake pipes of pleasure craft, ships, and power plants; massive consumption of the larvae of commercially important fish and shellfish and the food resources they rely upon; and incredible densities of jellyfish biomass that literally suffocate the stock in commercial fish farms.

Scyphozoans are entirely marine, with a reduced polyp phase and generally a large and conspicuous medusa phase. Unlike those of hydrozoans and
anthozoans, scyphozoan polyps are more or less unattached to one another and do not share nutrients with other colony members. Medusa formation is by a form of budding (strobilation), with the polyp typically remaining to continue budding and even to strobilate again. Scyphozoans are present from the shallowest intertidal to at least benthopelagic depths. There are three orders – Coronatae, easily distinguished by the presence of a coronal groove on the outer umbrella surface; Semaeostomae, typically with long, flowing oral arms and marginal tentacles; and Rhizostomae, which lack true marginal tentacles as well as a central mouth, instead having numerous tiny mouths on the edges of the oral arms.

The New Zealand Scyphozoa have never been definitively studied. The main references used for scyphozoan identification are Mayer (1910) and Kramp (1961), but many scyphozoans treated by Kramp have since proven to be more diverse than he had appreciated. A more recent study by Larson (1986) on the pelagic Scyphozoa of the Southern Ocean unfortunately excluded the Rhizostomae.

**Order Coronatae**

Coronates are one of the most abundant members of the midwater gelatinous zooplankton community, most often found at mesopelagic or benthopelagic depths, though a few species are found almost exclusively in shallow tropical waters. The systematics of the coronates is currently not well resolved, owing partly to the difficulty of obtaining specimens. Of the 40 or so currently recognised species, six medusa species have been found in New Zealand waters. Furthermore, one polyp species has been recorded numerous times, though it has not yet been linked to a particular medusa.

Coronates are easily distinguishable from all other medusa groups by the conspicuous coronal groove they possess on the exumbrellar surface. This ring separates the central thickened disc or dome portion of the body from the outer portion of radially alternating grooves and ridges. The ridges (termed pedalia) possess either sense organs (termed rhopalia) or tentacles. The tentacles are solid and can occur singly or grouped between rhopalia. Furthermore, coronates have a simple, short mouth, lacking the lobes characteristic of the Semaeostomae and Rhizostomae.

Coronates have not been reviewed systematically for about a hundred years, nor have they yet been examined even casually using molecular methods. The most recent taxonomic treatment of the pelagic coronates is by Larson (1986), exclusive to the Southern Ocean. The life cycles of the coronates are only recently becoming appreciated for their complexity and diversity of life habits. Most coronates have a scyphistoma (polyp) stage that is surrounded by a firm periderm tube. The polyp may be solitary or colonial. *Periphylla*, however, is now known to lack a planula larva, scyphistoma, and ephyra (newly budded medusa), instead developing directly from the embryo to the medusa.

Very little is known about the ecology of the coronates worldwide, but there have been some interesting recent studies. Fosså (1992) discussed an unusual shallow-water bloom of large coronates normally found in deeper waters; this bloom had serious effects on local Norwegian fisheries. Hunt and Lindsay (1998) reported that *Atolla* uses an enlarged tentacle to fish for prey, which is then taken into the opaquely pigmented gut, where bioluminescent responses are masked from the outside world.

**Order Semaeostomae**

Five species of semaeostomes have previously been documented in New Zealand waters, none endemic, though there are currently at least two new species from Stewart Island and one from the Marlborough Sounds awaiting description. Furthermore, the long-believed cosmopolitan distribution of some species (e.g. *Aurelia aurita*, *Cyanea capillata*, *Pelagia noctiluca*) (see Dawson 2003) is being re-examined, with the identification of cryptic and not-so-cryptic species being
found. Thus, it seems likely that additional species may be found among the New Zealand fauna, which appears to number about 11 species in total.

Semaeostome medusae are easily identified from other scyphozoans in that they most often have the 'typical jellyfish' appearance of a large, flattish or dome-shaped body, many marginal or submarginal filament-like tentacles, and long, flowing, fleshy oral arms emanating from the centre of the underside of the body. Semaeostomes are often conspicuously coloured, either solid or with mottling or radiating streaks. Most semaeostomes are thought to have a reduced polyp stage and a large medusa stage, but the life cycle of most species remains unknown. Semaeostome polyps are typically only one to two millimetres tall, lacking any sort of chitinous or calcified supportive structure, and with a terminal ring of tentacles. The polyps are asexually proliferated by side-budding, stolon budding, or formation of chitinous cysts (podocysts) from the attachment disc.

Among jellyfish in New Zealand waters, members of the Semaeostomeae have caused the most problems for commercial fish farmers, with the common moon jellyfish, *Aurelia* sp., being drawn into bays where fish are penned. The actual mechanism of death to the fish is not yet well understood, but is believed to be a combination of jellyfish mucus coating the gills and nematocysts irritating the fish and increasing respiration rate.

**Order Rhizostomeae**

Five rhizostome species have been recorded in New Zealand waters, three endemic. Unfortunately, New Zealand rhizostome systematics is in complete disarray. Mayer (1910) regarded Haeckel’s (1880) New Zealand endemics, *Archirhiza aurosa* and *Cannorhiza connexa* in the family Archirhizidae, to be ‘apocryphal.’ Mayer further believed that Haeckel’s (1880) other New Zealand endemic, *Leonura leptura*, was just another name for *Leonura terminalis*, which he then promptly reduced to a junior synonym of *Leptobrachia leptopus*. By the time of Kramp’s (1961) synopsis, only two rhizostome species were recognised in New Zealand, neither endemic. Present-day rhizostome classification was established by Stiasny (1921, 1923) but has been the subject of much debate. One of the more interesting questions currently under investigation is whether the Rhizostomeae is polyphyletic, arising from different groups of semaeostomes.

Rhizostomes are characterised by lacking marginal tentacles (though one species from the Philippines and Australia has tentacle-like elongations of the marginal lappets), and by the absence of a central mouth, which is present in all other medusae. Instead, the oral arms are covered with small mouthlets, used to ingest tiny bits of food. The oral arms may be thin and flexible or tough and rigid. Some have thickened areas near the top, called scapulettes or epaulettes.

Very little is currently known about the ecology and life history of most rhizostomes. They are primarily tropical, but a few are subtropical. Many species have symbiotic zooxanthellae (dinoflagellates) in their tissues, which may supply an important portion of the host’s nutritional requirements. Some species of zooxanthellate rhizostomes appear to position themselves in sunlit areas, oral side up, possibly to maximise exposure of the zooxanthellae to light. In cases where the life-cycles are known, the species all possess both a polyp and medusa. During strobilation, many rhizostomes produce only a single ephyra at a time (monodisc strobilation), whereas some produce numerous ephyrae simultaneously (polydisc strobilation). Asexual polyp proliferation is accomplished by podocyst formation or ciliated planuloid budding.

Rhizostomes are among the most economically important medusae, with fisheries developed in several countries. A few instances of rhizostome invasion and economic loss have been recorded among some species in Western Australia and the Gulf of Mexico, but they do not seem to have yet caused damage in New Zealand.
Class Staurozoa

Order Stauromedusae
The Stauromedusae are benthic, being attached to seaweeds, rocks, and firm objects by a long, trumpet-shaped column with an adhesive base. They typically have eight arms, each with a terminal cluster of short, clubbed tentacles, but considerable variation exists on this basic form. The creeping planula is distinct compared with those of all other cnidarians, lacking cilia and having a fixed number of endodermal cells.

Very little is currently known about the ecology and natural history of the stauromedusae. They appear to prey upon a variety of small crustaceans and molluscs. Stalked medusae make up a minor part of the shallow subtidal community in many temperate regions, but they have been found in nearly all parts of the world and at great depths. In shallow water, they are typically found on eelgrass or seaweeds, and display striking cryptic coloration. Stauromedusae are capable of creeping as well as somersaulting, but are not capable of swimming in typical medusoid fashion. To date, only a single stauromedusan life cycle is known. In contrast to scyphomedusae, they appear to lack strobilation; the non-ciliated planula larva develops into a polyp, which develops directly into the mature medusa. Asexual proliferation of the polyps is accomplished by budding.

The systematics of the Stauromedusae was recently re-examined by workers in America and Brazil (Marques & Collins 2004) who concluded that the group is independent of the Scyphozoa, based on morphology of the gastrovascular system, planula larva, sperm, ovary, and nucleotide sequences.

Only a single stauromedusan species, *Craterolophus macrocystis*, had been documented in New Zealand waters. Originally described from Port Chalmers, near Dunedin, on the kelp *Macrocystis*, it has apparently never been found again. Like most stauromedusans, *C. macrocystis* is less than 25 millimetres tall; it is further described as being deeply bell-shaped, with the stalk about two-thirds the bell height. It has eight arms and is dark green when alive, and thus well camouflaged on its kelp substratum. A second stauromedusan, *Depastromorpha africana*, was recently reported to occur in New Zealand waters by Grohmann et al. (1999), an unidentified species of *Lipkea* has been found on rock walls in submarine caves at the Poor Knights Islands and in Fiordland (Wing 2008, as *Cassiopeia*), and a species of *Kishinouyea* was photographed on kelp at Stewart Island.

Fossil staurozoans in New Zealand are represented by the wholly extinct conulariids, recently united with Stauromedusae in the new class Staurozoa (Marques & Collins 2004). Conulariids had conical exoskeletons that were square in cross section.

Class Cubozoa – box jellies

Order Cubomedusae
The Cubozoa is a minor, entirely marine class in the Cnidaria, with only 17 currently recognised species worldwide. Until recently, it was considered to be an order of the Scyphozoa and was only recognised as a separate grouping when studies of the life cycle revealed total metamorphosis of the polyp into the medusa. Additional differences from the other classes have since been noted, such as highly complex eyes with lenses and retinas, pigment spots on the planula that may serve a photosensory function, and sophisticated behaviours including purposeful avoidance of dark objects and copulation with sperm transfer.

The structure of the cubozoan medusa is relatively simple, yet complex relative to other medusa body plans. The body (or bell) is typically quite muscular, and is cuboid or elongated, but still squarish in cross section. The aperture of the bell is narrowed by a shelf-like projection, called a velarium, thought to aid the animal in jet propulsion. On each of the four corners is attached one
or more pedalia, the fleshy base of the tentacles. The pedalia may be branched, as in chirodropids, or simple, as in carybdeids. The tentacles are hollow, highly extensile, and contain many rings of nematocysts. Nematocysts may also occur on the exumbrella of some species. The toxins contained in the nematocysts of cubozoans are not well understood but in all cases are capable of causing pain and rash, and frequently more severe local or systemic reactions. The cubozoan mouth is situated upon a short or long manubrium, and thus may hang down into the bell cavity. The stomach is separated from the gonads, the former being in the upper portion of the bell, and the latter being typically leaf-like and attached at their midline down the entire side of each corner of the body. In some chirodropids, however, the gonads are instead located on structures along the flat inner facets of the bell. Cubozoan sensory structures (rhopalial), each typically containing six eyes plus a balance organ, are located singly on each flat side of the bell.

Only one species of cubozoan is known from New Zealand waters, the diminutive *Carybdea sivickisi*, found in Cook Strait (Hoverd 1985). This species, which reaches about 10 millimetres bell height, is relatively common in coastal tropical regions throughout the Pacific. On Australia’s Great Barrier Reef, it is rarely found except during the annual coral spawn, when it occurs in abundance. Elsewhere it is typically found at night, apparently spending the day attached to stones and algae by the adhesive pads on the exumbrella.

Very little is known about cubozoan ecology and behaviour, and we should remain cautious about broadly applying these few facts. Some cubozoans feed on active prey such as small crustaceans or fish. The seasonal cycle of *Chironex fleckeri* in Australia appears to be intimately tied to the wet season in the tropics, with the species apparently overwintering in polyp form in the rivers and then metamorphosing to the medusa and being washed out with the onset of the rainy season. Many cubozoans are photopositive, being drawn to various forms of artificial lights at night. Anecdotal reports abound of cubozoans schooling, co-operatively hunting, stalking prey, and responding to certain shapes and other visual cues – these reports are intriguing and should be tested scientifically. Whether or not these curious behaviours are verified, cubozoans present a most interesting paradox, possessing image-forming eyes while lacking a recognisable brain.

Cubozoan systematics has recently been revised, with numerous new species being added (Gershwin 2005). Under the new system, two orders – Carybdeida and the Chirodropida – comprising six families, are recognised. The order Carybdeida now contains 17 species, with several more awaiting formal description. Only one is presently known from New Zealand waters. Members of this order are easily distinguished, possessing a single tentacle to each arm-like pedalium, though more than one pedalium may be present at each corner. The remaining 10 cubozoan species belong to the Chirodropida. These animals have numerous tentacles on each of the four pedalia, and there is no species with more than one pedalium on each corner. This order contains the most dangerous animal on earth, the deadly Australian box jellyfish, *Chironex fleckeri*. No members of this order have been found in New Zealand waters.

**Class Hydrozoa – hydroids and their medusae**

The large class Hydrozoa includes marine and freshwater hydroids, some calcified and coral-like, and their medusae, as well as the colonial, highly polymorphic creatures of the plankton known as siphonophores. The class contains around 3,200 species (Schuchert 1998). The higher classification of Hydrozoa is currently in a state of flux as phylogenetic studies try to elucidate monophyletic groups. Some modern classifications rank former orders or even suborders as subclasses, while other orders (those containing coral-like hydroids) have been
reduced to families. Recently, the Hydrozoa has been regarded as comprising two distinct subclasses – Leptolida (hydroids and their medusae) and Siphonophora – implying that the latter is a sister group to all other Hydrozoa, which is not the case, as the Siphonophora is related to the athecate hydroids (Anthoathecata). The classification used here is based on a more recent approach using gene-sequence data (Collins 2000) that gives evidence of two major clades of Hydrozoa – the Trachylina, consisting of Limnomedusae, Narcomedusae, and Trachymedusae; and the Hydroidolina, comprising Leptotheclata, Anthoathecata, and Siphonophora. The affinities of the Laingiomedusae in this scheme are uncertain.

Hydrozoans are remarkably varied. They may be solitary or colonial, with polyp and medusa phases, or either phase may be lacking altogether. In many species the life cycle is still unknown or inadequately known, such that polyp and medusa phases have not yet been linked and are known by separate names. The form and anatomy of the polyp and medusa, and the types of nematocyst that they have, are the basis of classification into a number of orders (or subclasses). The medusa may be thought of as comprising an umbrella (the bell-like upper body), beneath which is a projecting sac-like manubrium, the opening of which is the mouth and its cavity the ‘stomach’. From the manubrium run the radial canals that connect with the circular canal around the umbrella margin, or both radial and circular canals may be modified or lacking.

**Order Limnomedusae**

This small order of mostly marine forms also contains some freshwater species and used to be included in the Trachymedusae. Limnomedusae differ in having a polyp stage, but this is very diminutive and colonial. The medusa is similar to that of trachymedusans but gonads are attached to the manubrium in *Limnocnida* and there is a tiny colonial polyp stage. Hollow tentacles are borne on the margins. Two species are found in New Zealand. *Craspedacusta sowerbyi* was first discovered in 1880 in Kew Gardens, London, in a botanical pond planted with the Amazonian waterlily *Victoria regia*. Later findings of the medusa in other European botanical ponds containing the same waterlily support the supposition that the cnidarian was brought from Brazil with the plant. The medusa is now widely reported from around the world, including New Zealand, where swarms were first noted in 1956 in lakes of the Taupo Volcanic Zone. To date, medusae have been found in volcanic Lakes Taupo, Tarawera, Rotorua, Rotoiti, Ngapouri, Rotoehu, and Pupuke, and hydro Lake Maraetai. The largest was two centimetres diameter; the polyp stage was discovered in a Dunedin aquarium in 1962 (Fish 1971, 1975).

A second limnomedusan species was discovered in Lake Pupuke in Auckland in March 1999. A young collector reported fertile specimens up to seven centimetres diameter; infertile specimens (not preserved) were photographed by Auckland zoologist Peter Jenkins and the photos sent to one of the authors (P. Schuchert). The medusae appear to belong to the genus *Limnocnida*, which mainly occurs in the great African lakes but the relatively small diameter of the stomach does not fit the descriptions of any of the known four species. It may be new.

The marine family Proboscidactylidae has been included in the Limnomedusae by some authors. Following Schuchert (1996) and Bouillon and Barnett (1999), it is here listed under order Anthoathecata.

**Order Laingiomedusae**

This small, relatively newly segregated order (Bouillon 1978) includes planktonic marine medusae with the umbrella margin slightly lobed, owing to four radial furrows where the solid tentacles arise. Gonads occur as four masses on the manubrium or interradial pockets therein. Reproduction has never been studied so it is not known if there is a polyp phase. The sole New Zealand species,
endemic *Fabienna sphaerica*, is known from Wellington Harbour, Devonport, and the Leigh marine reserve (Schuchert 1996; Bouillon & Barnett 1999).

**Order Narcomedusae**
The medusa is the dominant or only phase, and the umbrella margin is distinctively scalloped by indentations where the solid tentacles emerge some distance above the margin. The umbrella is generally flatter than in other orders, and the mesogloea occurs as a lens-like mass in the centre that thins towards the sides. The manubrium is usually very broad and often pouches; gonads occur either on the manubrium walls or on the pouches. Radial and circular canals are usually lacking. Bouillon and Barnett (1999) illustrated the 14 species that are presently known in New Zealand waters. All are widely distributed in the major oceans of the world, where they prey on plankton. The largest local species is *Solmissus incisa*, which can attain an umbrella diameter of 10 centimetres.

**Order Trachymedusae**
The medusa is the only phase in this order. The umbrella is hemispherical or deeply bell-shaped and the solid or hollow tentacles spring from the unscalloped margin. The manubrium is narrower than in narcomedusans and unpouched. There is a circular canal and radial canals; gonads are attached to the latter. Bouillon and Barnett (1999) illustrated 19 species found in New Zealand waters. All are planktonic carnivores, widely distributed in the major oceans of the world. The largest local species is *Halistrephe maasi*, which can attain an umbrella diameter of 10 centimetres.

**Order Leptothecata**
By far the largest order of Hydrozoa, the leptothecates (thecate hydroids) are wholly marine and mostly polypoid. A number have both polyp and medusa phases. The former is colonial and covered in a chitinous perisarc secreted by the outer cellular layer of the body, the ectoderm. Colonies consist of stolons attached to the substratum (rocks, algae, other organisms, wharf pilings, boat hulls, etc.) from which arise hydranths or erect stems bearing hydranths – the feeding polyps. They consist of a sac-like body with a short, proboscis-like hypostome opening at the mouth; one or more whorls of tentacles surround the hypostome. In the suborder Conica the hypostome is conical or dome-shaped; in the suborder Proboscoida it is globular. The perisarc surrounding each hydranth forms a cup-like hydrotheca. During development, the hydrotheca is closed by a membrane that is lost in many species in adult life. In others, it develops into a closing apparatus (operculum) that, upon contraction of the polyp, folds over it for protection.

There are two other types of hydranth, the leptothecates being polymorphic. Reproductive structures are modified hydranths called blastostyles – elongated structures that either bud off free-living medusae or produce reduced medusae that are not liberated. In some cases the medusa is so reduced, with loss of tentacles and other structures, that virtually only gonads remain. The perisarc around each blastostyle forms a gonotheca. Another modified type of hydranth is the nematophore. It lacks tentacles, mouth, and stomach cavity but is richly armed with nematocysts, especially in the swollen distal part. The body of the nematophore may be unprotected or encased in a nematotheca. Nematophores are typically movable (e.g. families Lafoeidae, Plumulariidae, Halopterididae), but they can be fixed (Aglaopheniidae). They serve to protect the colony and possibly assist in the capture of food. In species where the medusa is fully liberated, the gonads are borne beneath the radial canals.

Colonies may be relatively small and simple or complexly branching and robust. Some are encrusting mats of ramifying stolons – hydrorhizae – directly giving rise to polyps. A few species send up a bundle of parallel stolons forming false stems. Most branched colonies have one main stem, the hydrocaulus, that
produces side branches with hydranths. The hydrocaulus may be straight or zigzag. It is usually single but can be thickly fascicled, in which case the true hydrocaulus is covered over by stolons or branches from below. Branching may occur in all planes, giving a bushy appearance, or in one plane, giving a fan- or plume-like appearance. In some species, gonothecae are restricted to special regions of the colony modified for their protection. In highly developed examples (e.g. Aglaophenia, Thecocarpus), the modified area may involve a reduction in hydrothecae, an increase in nematophores, and the development of special leaf-like branches forming a basket-like corbula.

The New Zealand leptothecate fauna currently stands at 252 species, of which 15 are not yet described or of uncertain identity (Vervoort & Watson 2003).

**Order Anthoathecata**
The Anthoathecata (athecate hydroids and anthomedusae) and Leptothecata (thecate hydroids and leptomedusae) were at one time grouped in the large order Hydroida. In the Anthoathecata the perisarc does not form thecae around polyps and gonophores and medusae bear their gonads on the manubrium. The coralline orders Milleporina (tropical forms not found in New Zealand) and Stylasterina are now understood to be calcified anthoathecates. Anthoathecates exhibit a greater range of form than leptothecates. In both marine and freshwater environments there are medusoid as well as solitary and colonial polypoid species. In some families and genera, either the medusa phase or the polyp phase is suppressed or unknown. New Zealand examples of solitary polypoid species include the freshwater hydras (family Hydridae), marine Candelabrum (Candelabridae), Hybocodon (Tubulariidae), Corymorpha (Corymorphidae), and the curious planktonic hydroid Pelagohydra (Schuchert 1996). The amazing Branchiocerianthus, a deep-sea form not yet discovered in New Zealand waters, has solitary polyps with stalks up to two metres tall. Colonial anthoathecates include small prostrate forms with polyps arising directly from creeping stolons, and large bushy colonies, like those of endemic Solanderia ericopsis, up to half a metre in height. The only colonial freshwater hydroid is Cordylephora caspia, which is widespread around the world in rivers and brackish inlets. Many species are mostly encountered as planktonic medusae only – either the polyp phase is diminutive and easily overlooked (e.g. genera Leuckartiara, Oceania, Rathkea) or unknown (e.g. genera Annatiara, Barnettia, Calycopsis, Cytaeis, Neoturris). Medusae of the Cladonematidae are frequently adapted for attachment to the substratum, and some can even ‘walk’ on their tentacles, which are branched with adhesive knobs. Three species are found in New Zealand. Whereas Cladonema radiatum medusae can swim and walk, those of Staurocladia vallentini and S. wellingtoni can only walk (Schuchert 1996). They are normally found on algae.

The anthoathecate family Porpitidae used to be classified among the Siphonophora. The oceanic species Porpita porpita and Velella velella (by-the-wind sailor) are both found in New Zealand waters, but only the latter is common. These are floating colonies, but medusae are also produced. Velella is distinguished from Porpita most noticeably by the sail attached to the float. Both species are strikingly blue and instantly recognisable when cast ashore on beaches (frequently those along the west coast of both main islands).

The families of Anthoathecata are grouped into two suborders. The Filifera are characterised by filiform tentacles, whereas Capitata generally have knobbled tentacles; there are also differences in the cnidae. The suborder Filifera includes the coral-like Stylasteridae (formerly order Stylasterina), one of five families of the superfamily Hydractinoidea. The New Zealand stylasterid fauna of 55 species (EEZ) is one of the most diverse in the world (Cairns 1991). Five species are found only in the Kermadec Islands (Cairns 1991). The largest and most striking New Zealand species is bright red Errina novaezelandiae, a protected
Some New Zealand thecate (A–G) and athecate (H–K) hydroids.


species found from Milford Sound to the Auckland Islands. It can branch up to 21 centimetres across.

Including the Styloasteridae, the New Zealand anthoathecate fauna currently comprises 150 species, of which 12 are unnamed or of uncertain identity.

Order Siphonophora

Despite the great attention paid to siphonophores during the nineteenth century, few people today have even heard of them, although mention of the Portuguese man-of-war might bring back some painful memories. So what are siphonophores? The name itself means ‘bearing stomachs or siphons’, but this gives few clues as to their nature. Wilson (1975) described them as ‘bizarre creatures . . . vaguely resembling jellyfish’. They are highly polymorphic hydrozoans with a number of specialised zooids that come in a bewildering variety of shapes and sizes. Their closest relatives appear to be in the order Anthoathecata. Wilson also considered them to be the ‘ne plus ultra of invertebrate social forms’. Although individual specimens are generally referred to as colonies, Wilson also noted that: ‘Much of the difficulty in conceptualizing . . . siphonophores as colonies rather than organisms stems from the fact that each of the entities originates from a single fertilized egg.’ He further added: ‘The resolution of this paradox is that siphonophores are both organisms and colonies. Structurally and embryonically they qualify as organisms. Phylogenetically they originated as colonies.’ This point is discussed further by Mackie et al. (1987).

There are about 160 known species of siphonophore, although, with the advent of in situ collection using submersibles or remotely operated vehicles (ROVs), many as-yet-undescribed ones have been found. They are exclusively marine and most species are pelagic (living below the ocean surface). The most famous exception, and the first species to be described, is the Portuguese man-of-war, Physalia physalis, which floats at the surface and whose tentacles, hanging down for tens of metres through the water, can inflict a powerful sting. Another small group, the rhodaliids, have adopted a benthic lifestyle by using their tentacles to anchor themselves to the seabed, while their relatively enormous float (pneumatophore) suspends them above it like a tethered hot-air balloon. One of these species has been found off New Zealand. Both Physalia and the rhodaliids have undergone great morphological changes in response to their adopted lifestyles. Most pelagic species, however, consist of a narrow hollow stem to which are attached many, in some cases thousands, of individuals (zooids) that are specialised to perform particular functions such as propulsion, feeding and digestion, protection, and reproduction. The length of this stem varies from a few millimetres to many tens of metres, depending on the species, and some are probably the longest animals in the world.

The main treatise on siphonophore taxonomy is by Totton (1965), with more limited information being found in Kirkpatrick and Pugh (1984) and Pugh (1999). The order Siphonophora is divided into three suborders. The Cystonectae includes the Portuguese man-of-war and only four other pelagic species. They are characterised by having a large (enormous in the case of Physalia) apical float with a terminal pore, and a stem, with a single budding zone, that bears only feeding and digestive gastrozooids (each with a single tentacle) and sexual zooids. The latter comprise gonodendra bearing sexual medusoids (gonophores) and some asexual swimming bells and gonopalpons. Each specimen bears gonophores of only one sex. One of the many curious features of siphonophores is that the gas secreted into the float is carbon monoxide. The float has a chitinous lining to prevent escape of the gas by diffusion and to protect the remainder of the animal from its potentially lethal effects.

Siphonophores in the second suborder, Physonectae, are basically much more complicated versions of the pelagic cystonect design. They have a smaller apical float that does not usually have a terminal pore. The size of the float is apparently
insufficient to give buoyancy to the whole animal and probably functions as a sensory organ, indicating to the animal which way is ‘up’. There are two budding zones. The first, immediately below the pneumatophore, generates a series of identical swimming bells (nectophores) – modified asexual medusoids – that are used for propulsion. Below this series of nectophores, called the nectosome, is the second budding zone. This produces a variety of zooids. In addition to the gastrozooids and tentacles and gonophores (but without asexual nectophores and, often, gonopalpons) present in cystonects, there are protective bracts, whose medusoid or polypoid origin is uncertain, and reduced gastrozooids (palpons), which probably play a part in digestion and excretion. This part of the stem is called the siphosome. The zooids here are arranged into repeated series called cormidia, with each cormidium containing a single gastrozooid and tentacle and a variable number of the other elements. Depending on the species, each specimen may bear gonophores of both sexes or only one. Some physonects have undergone gross morphological changes, in that either the siphosome (family Physophoridae, and Melophysa melo in the family Athorybiidae) or both the nectosome and siphosome (family Rhodaliidae) have become coiled up and fused together to form a corm. The latter also has occurred in Athorybia (Athorybiidae), but there the nectosome has been lost entirely.

The third suborder, the Calycophorae, differs markedly from the previous two in that no apical float is developed. The nectosome is, in most cases, reduced to two dissimilar nectophores that are juxtaposed one above the other. In the family Prayidae, however, there are usually two similar nectophores that lie opposite each other, while in the Hippopodiidae up to about 15 flattened nectophores are arranged into a semi-spherical structure. There are, as is always the case with siphonophores, other exceptions to the general rule. The siphosome is relatively simple, with each cormidium reduced to a single bract (absent in the Hippopodiidae) and gonophore, in addition to a gastrozooid and tentacle. Palpons, with possibly one exception, are absent. In many calycophorans the distal cormidium breaks free from the stem and lives a separate life. This is called the sexual, or eudoxid, stage.

There have been no definitive studies of the New Zealand Siphonophora, and arriving at a species list has been challenging. Historically, the first record appears to be that of Quoy and Gaimard (1834), who described a species by the name Stephanomia imbricata. Later authorities (e.g. Bigelow 1911) have regarded it as a doubtful species, although one could interpret the figures as representing part of the siphosome of Agalma elegans. The latter species is included in the present listing. Nothing further was published until Hutton (1880) recorded three previously described species. Then, from the material collected by the Challenger Expedition, Haekel (1888) recorded two species in New Zealand waters, one a rhodaliid physonect, Stephania bathyphysa, while the other, Desmalia imbricata, was not described and therefore is a nomen nudum. For the rhodaliid, many subsequent authorities, including Totton (1965), tentatively synonymised it with another of Haekel’s rhodaliid species, Stephanalia corona. Pugh (1983) suggested, however, that although Haekel’s description was inadequate, there might possibly be morphological differences. In addition, rhodaliid species appear to have relatively restricted geographical distributions. Since S. corona has been found only in the northeastern Atlantic, Pugh decided to retain S. bathyphysa but moved it into the genus Stephanalia. There was then a hiatus until Totton (1954), in a publication on the siphonophores of the Indian Ocean, also included New Zealand records of some species. Margulis (1987) also listed some siphonophores collected in New Zealand waters, based on data in an obscure Russian PhD thesis produced by V. A. Barkhatov. Margulis listed 13 of the 29 species that Barkhatov apparently identified. Although through the kindness of Dr Sofia Stepanjants the thesis has been located, it has so far proved impossible to obtain even a basic species list from it.
The only other publication that has been found to contain records of siphonophores in the New Zealand region is that of Alvariño et al. (1990). This work must be treated with great caution, as it is liberally sprinkled with errors and includes many species that Alvariño herself established, none of which is presently considered to be valid. Synonymising these with established species has yielded a few extra names for the New Zealand region. *Bargmannia elongata* in Alvariño et al.’s (1990) list is referred to in the checklist below as *Bargmannia* sp. because it is impossible to know to which species they were referring.

This dearth of information means that only 49 species of siphonophores appear to have been identified from New Zealand waters. A concerted effort to collect and study siphonophores in the EEZ ought, however, to double the number of species. Only *Stephalia bathyphysa* (Rhodaliidae) is presently endemic to New Zealand, but this may only be the result of the lack of information on these creatures.

Siphonophores are ubiquitous throughout the world’s oceans and, although most species are epipelagic, they have been found at all depths down to at least 5,000 metres. The epi- and mesopelagic species can be broadly categorised as boreal, temperate, or tropical, although some span all three ranges. In the northeastern Atlantic, there appears to be a good correlation between the latitudinal and depth distribution of siphonophores and the various water masses present (Mackie et al. 1987). In addition, maximum numbers of species are found at about 20° N, with a steady decline in numbers towards the pole. There are too few data to establish whether the same trend occurs in the southern hemisphere, however. Siphonophores do not live in regions of reduced salinity and so most are truly oceanic, but a few occur almost exclusively in shallower inshore waters where there is no reduction in salinity.

All siphonophores are carnivores and frequently exist in such numbers that they are the dominant such group (Pugh 1984). They capture prey using their tentacles, each of which is attached to the base of a stomach, or gastrozooid. There may be several hundred of these arranged down the stem. The tentacles, which usually have side branches (tentilla), are strongly armed with various types of nematocysts that, when discharged, either penetrate soft-bodied prey and inject a toxin, or stick to or wrap around the hard external skeleton of animals such as crustaceans. Once immobilised, the prey is transferred to one or more gastrozooids, which expand to enclose it completely (Mackie et al. 1987). Whereas most jellyfish capture their prey while swimming, siphonophores are passive feeders and wait for prey to bump into their tentacular webs. These webs, often complex, are set during brief swimming periods, which can culminate in choreographed spinning and spiralling movements. The encounter volume of these webs may be half a cubic metre (Madin 1988) or more for large physonect species. Some species also lure their prey by various means such as ‘squid jigging’, when individual tentilla are periodically contracted and then relaxed, or by use of aggressive mimicry (Purcell 1980; Pugh 1989, 2001) in species where the tentilla resemble and behave like other animals, such as copepods or larval fish.

Most calycophoran species feed on small crustaceans, especially copepods. Hippopodiids appear to feed exclusively on ostracods (Purcell 1981a), and a striking relationship between their depth distribution and that of their preferred prey has been found (Pugh 1991). Physonects tend to feed on a wide size range of crustaceans, but apolemiids include gelatinous organisms in their diet and others feed on small fish. Cystonects feed exclusively on soft-bodied organisms, mainly fish larvae, and the Portuguese man-of-war can eat more than a hundred items per day. Concentrations of these animals may have a considerable impact on fish stocks (Purcell 1981b). Although predators, siphonophores are not a trophic sink, since many other gelatinous carnivores, such as medusae, comb jellies, and planktonic molluscs, as well as many fish and turtles are known to feed on them. A variety of animals are also known to associate with siphonophores, but none has been reported in New Zealand waters.
Class Myxozoa

The Myxozoa (literally, slime animals) are obligate parasites of marine and freshwater fish and freshwater bryozoans. They have also been reported rarely in amphibians, reptiles, in the brain of a mole (Kent et al. 2001), and in an HIV-positive man. Where known, myxozoan developmental stages (actinosporeans) are generally parasitic in marine and freshwater annelid worms (tubificids and polychaetes). Myxozoans inhabit hollow organs such as gall and urinary bladders, in which case they are amoeboid, or they live in connective tissue or among the cells of the skin, gills, kidneys, liver, spleen, brain, gut, or muscle, where they either soon become encysted by layers of host tissue or spread diffusely, even dividing into fragments. They can be relatively harmless to the host but may cause damaging tumour-like masses or liquefaction of tissue. It is probably this last effect that elicited the name Myxozoa (from Greek myxa, slime, mucus). Unsightly cysts or softening of flesh lowers market value in fish species. Some myxozoans cause parasitic castration of hosts or affect organs badly enough to cause disease or mortality.

In older literature, myxozoans were classified as order Myxosporidia of subclass Cnidosporidia in the protozoan class Sporozoa. As these names imply, myxozoans have spores. It was early recognised that curious structures in the spores, called polar capsules, closely resemble the nematocysts (cnidae) that are found in cnidarians. Once in a host gut, digestive juices or some other stimulus cause the polar capsules to discharge, fastening the spores to the wall of the digestive tract. The spores hatch (i.e. the protoplasm exits, amoeba-like) through the gut wall into the bloodstream, which transports them to various tissues. Once settled, the ‘amoeba’ grow into a multinucleate phase – plasmodia, or hollow sacs, in which infective spores are produced. Myxozoans are generally classified according to details of their spores, the number of polar capsules/cnidae, and the number of valves through which these are discharged.

Recent ultrastructural and molecular work had seemed to demonstrate that myxozoans are highly derived parasitic cnidarians (Kent et al. 2001). Their polar capsules appear homologous with nematocusan nematocysts, and there are other characters linking them with multicellular animals (metazoans), including multicellularity, the type of cellular junction, and collagen production (Siddall et al. 1995). Among metazoans, the peculiar nematocusan Polypodium hydriforme, a parasite of sturgeon eggs, was reported to be closest in morphology and ribosomal genes to myxozoans (Raikova 1994; Siddal et al. 1995). Other molecular evidence supported a relationship with the Bilateria (metazoans with bilateral symmetry) (Smothers et al. 1994; Anderson et al. 1998). Recent work further suggested that, despite the presence of the cnidae-like polar capsules, myxozoans are derived from worm-like animals, possibly related to nematodes. Now, further molecular analysis demonstrates conclusively that myxozoans are indeed highly reduced cnidarians (Jiménez-Guri et al. 2007).

The trail of discovery nicely illustrates the way science works. An ecological study of freshwater bryozoans in England yielded a new type of myxozoan parasite, Tetracapsula bryozooides, that forms soft spores with four polar capsules in large spore-producing sacs in its bryozoan host, Cristatella mucedo (Canning et al. 1996; Okamura 1996). Further work on bryozoans uncovered a second species, T. bryosalmonae, in the bryozoans Fredericella sultana and Plumatella emarginata (Canning et al. 1999). Importantly, molecular sequencing of the 18S subunit of ribosomal DNA showed that T. bryosalmonae was the previously unidentified PKX organism that causes proliferative kidney disease (PKD) in wild and farmed salmonid fish in the northern hemisphere. Clarification of details of the life history of PKX revealed so many differences between Tetracapsula and other myxozoans that a high-level taxon, Malacosporea, was erected for this genus (Canning et al. 2000). Next, experimental trials successfully transmitted T. bryosalmonae from infected F. sultana to rainbow trout (Feist et al. 2001), backing
the findings from the molecular work (see also Tops & Okamura 2003).

The next clues in the trail of discovery concerning the morphological diversity of myxozoans were obtained from North America, where the ecology of Tetracapsula was further investigated (Okamura et al. 2001). Colonies of the bryozoan Hyalinella punctata in Ohio were found to contain a rare and peculiar worm-like parasite, Buddenbrockia plumatellae, first described in 1910 from Plumatella species in Belgium and subsequently found in Germany and Turkestan. Having muscles, but no gut or central nervous system, Buddenbrockia always had been impossible to classify, even to phylum level. Now, with fresh material from Ohio and newly found specimens in France, this organism could be studied using electron microscopy and molecular sequencing. Astonishingly, Buddenbrockia was discovered to have myxozoan polar capsules resembling those of Tetracapsula (Okamura et al. 2002). What is more, molecular evidence showed that B. plumatellae is none other than an unexpected vermiform stage of T. bryozoides, hinting at a complex life cycle (Monteiro et al. 2002). Differing at the generic level, the PKX organism was renamed Tetracapsuloides bryosalmonae (Canning et al. 2002). A vertebrate host has not yet been identified for B. plumatellae, and a worm-like phase has not yet been found for T. bryosalmonae. So far, these two species are the only known malacosporeans.

Monteiro et al. (2002) suggested the following evolutionary scenario for the Myxozoa. The latest common ancestor of all myxozoans had a vermiform phase in its life history, and probably a non-motile stage specialised for production of infective spores. After divergence of this evolutionary branch (clade) into myxosporeans and malacosporeans, animals in the former group lost all vestiges of the worm-like body plan. Instead, they evolved into plasmodia in which the spores develop. By contrast, some malacosporeans, at least, retained the capacity to develop both the worm-like form and a sac-like spore-producing form. (For a different interpretation – Polypodium and Myxozoa as basal bilaterians – see Zrzavý & Hypša (2003).)

Finally, Jiménez-Guri et al. (2007) have demonstrated that Buddenbrockia falls clearly within the Medusozoa (non-anthozoan Cnidaria), based on gene sequencing. To date, some 1,350 species of myxozoans have been described worldwide, in about 52 genera, but it is likely there are as many myxozoan species as there are fish species.

The New Zealand myxozoan fauna
Some 66 myxozoan species (9 freshwater, 57 marine), including 21 species not yet described or of uncertain identity, are known to parasitise New Zealand fish (Hine et al. 2000). Among the most serious is Myxobolus cerebralis, which causes whirling disease in salmonids (see www.whirling-disease.org) by attacking cranial cartilage, thereby affecting the balance organs. Whirling disease has been recorded in New Zealand rainbow trout (Oncorhynchus mykiss), Chinook salmon (Oncorhynchus tshawytscha), brown trout (Salmo trutta), and brook trout (Salvelinus fontinalis) (Hewitt 1972; Hewitt & Little 1972; Boustead 1982, 1993; Hine et al. 2000). Other freshwater fishes infected by myxozoans include eels, some whitebait species, and torrentfish. Little is known about myxozoan life histories in New Zealand. Based on an overseas study, there is circumstantial evidence that some species may be able to transmit directly between fish (Diamant 1997). Hine et al. (2000) listed all known New Zealand myxozoans, their hosts, and the tissues in which they have been found.

The first records of New Zealand species were those of Laird (1953), who studied the parasites of intertidal fishes. Next came the large and detailed work of Meglitsch (1960, 1968, 1970), who described 33 new species and mentioned other species not able to be identified or named. Building on this work, Hewitt (1972), Hewitt & Hine (1972), Hewitt & Little (1972), Hine & Boustead (1974), Hine (1975, 1977, 1978a,b, 1979, 1980), and Boustead (1982, 1993) reported other species associated with marine and freshwater fishes.
Most New Zealand myxozoans infect bottom-feeding fish. The only pelagic species infected are kahawai with *Leptotheca* sp., blue mackerel with *Ceratomyxa* sp., jack mackerel with *C. inconstans*, bellowsfish with *C. conscripta*, and silver dory with *C. declivis* (Hine et al. 2000). During the late 1980s and 1990s, there was an expansion of marine fish aquaculture in many parts of the world, including New Zealand, particularly net-pen culture of salmonids and sparids. As a consequence of this expansion, several myxozoans have been recognised or elevated in status as important pathogens. However, while increased research has advanced knowledge of development and pathogenesis overseas, this effort has not been matched by equivalent work in New Zealand. Among diseases of importance to aquaculture in New Zealand, Diggles et al. (2002) mentioned *Myxidium* disease of snapper (*Pagrus auratus*), so far known only from the east coast north of Auckland.

Proliferative kidney disease of salmonids is not yet known in New Zealand, but potential bryozoan hosts are – there are six species of phylactolaemate bryozoans in New Zealand fresh waters, including *Fredericella sultana* and *Plumatella emarginata*. Freshwater bryozoans produce dormant structures called statoblasts, encysted capsules of tissue that can be easily transported by migratory waterfowl. It is not inconceivable that PKD could be introduced to New Zealand in this way, but more work is needed to ascertain the likelihood. At present, bryozoan statoblasts are not known to become infected by the PKX organism.

**New Zealand fossil Cnidaria**

**Paleozoic**
The oldest-known New Zealand fossil cnidarians are a hydroid (Skwarko 1962) and rugose and tabulate corals. Ordovician coral faunas are known only from the Northwest Nelson area, specifically the Arthur Marble (Arthur Marble 2 of Webby et al. (1981)) in the Takaka valley, first reported by Park (1890), then by Benson and Keble (1936). Cooper (1965, 1968) listed numerous localities where coral and other faunas had been found. Essentially the same coral list was reproduced by Suggate et al. (1978) and Webby et al. (1981).

This general fauna is very similar to well-known east Australian faunas. According to Webby et al. (2001), the Northwest Nelson fauna is Eastonian or early Bolindian in age (c. 439–460 million years ago (mya)). Sparse conodont data from the Arthur Marble do not allow a refined age, but at Hailes Knob in the Takaka Valley the Arthur Marble (at least 300 metres thick) is overlain by the Hailes Quartzite from which Silurian brachiopods are known; at one locality the Arthur Marble is underlain by the Wangapeka Formation, which has yielded Gisbornian (c. 460–469 mya) graptolites; the age of the formation was discussed by Webby et al. (1981).

More recent study of the poorly preserved material confirms the presence of the tetracorals *Favistina* (= *Favistella* of previous lists) and *Grewingkia*; and the tabulate corals *Nycotopora*, *Foerstephyllum*, *Proheliolites goldfussi*, *Plasmoporella*, and at least two species of Halysitidae.

Early Devonian reef-building corals are known from the Reefton district (Hill 1955), where eight species have been recorded, indicating a mix of solitary, massive, and branching forms providing the structural framework for a range of other organisms including bacterial/algal stromatoporoids that also contributed to reef structure (Fagerstrom & Bradshaw 2002). Devonian corals are also known from Baton River, Nelson (Shirley 1938).

Four genera of rugose coral and two genera of tabulate coral were described by Hill (1952) from calcareous Late Permian rocks in Southland. Two Permian reef-building species were reported from limestone in the vicinity of Whangaroa Heads, Northland (Leed 1955). Subsequently, Vachard and Ferrière (1991) recorded a rugose coral (*Pavastephyllum*) and a tabulate (*Sinopora*) from Whangaroa Bay. Hada and Landis (1995) found an undetermined polycelcid and an undescribed species of *Taisyakuphyllum* from another limestone association in South Canterbury.
Fossil staurozoans of Permian age are represented by conulariids. Like modern Stauromedusae, conulariids were attached. Though rather uncommon, they occur in certain horizons of Late Permian age. Waterhouse (1979, 1986) has recorded and/or described two genera (*Paraconularia* and *Gondaconularia*) and three species of conulariid from New Zealand.

**Mesozoic**

Certain colonial organisms found in the Late Triassic in New Zealand are apparently cnidarians of uncertain hydrozoan affinity (Schäfer & Grant-Mackie 1998). *Heterastridium conglobatum* is interpreted as having had a pelagic-planktonic life in the open ocean, forming spherical colonies 20 millimetres in diameter. In contrast, *Eoheteropora maorica* (first described as a bryozoan in the genus *Monotrypella*) was an encrusting tabulate coral. It is significant that this finding of *Eoheteropora* is considered to be the only record of a tabulate coral following the massive end-Permian extinction event. *Heterastridium conglobatum*, a cosmopolitan species, is also known from New Caledonia.

The earliest New Zealand scleractinian corals are of Jurassic age. Two small unidentified colonies are known from the Temaikan (Middle Jurassic) of the Awakino Valley, Mahoenui, and an undetermined species of *Caryophyllia* sensu lato was collected in Ohauan beds (Late Jurassic) at Kawhia and Port Waikato (Hudson 1999). Scleractinians are also known from the Early Cretaceous. Squires (1958, 1962a) described eight Cretaceous species; only two more have been discovered since then, and they remain undescribed. One species, *Dasmosmilia? spissa*, apparently survived the end-Cretaceous extinction event, surviving into the Paleocene (Squires 1958). According to Squires, the Cretaceous corals, though mostly endemic, have affinities with species in North and South America.

Fossil staurozoans of Triassic age are represented by conulariids, which became extinct prior to the onset of Jurassic time. Marine Triassic sequences in New Zealand, and also New Caledonia, appear to have some of the earliest-known fossils of this rather obscure group of chitinophosphatic shells. Though rare, they occur in certain horizons of Late Triassic age. Waterhouse (1979, 1986) has described three genera and three species of conulariid from New Zealand. One genus, *Flectoconularia*, appears to be endemic, whereas the other two (*Paraconularia* and *Gondaconularia*) appear to be cosmopolitan.

**Cenozoic**

The diverse Cenozoic cnidarian fauna, mostly comprising stony corals, has been the subject of several detailed studies (e.g. Squires 1958, 1960b, 1962b; Hayward 1977; Brook 1983; Cairns & Grant-Mackie 1993). Paleocene and Early Eocene hexacoral diversity is relatively low, whereas by the Middle Eocene the fauna is greatly expanded and shows affinities with Australia, the Tethys, and the American Mediterranean. By the Middle Oligocene, the Eocene faunas had reached their greatest diversity and there was a notable abundance of octocorals. Late Oligocene diversity became reduced because of cooling seas and increasingly sediment-laden waters. An invasion of Indo-Pacific corals, including warm-water zooxanthellate species, marks the beginning of the Miocene. Warm-water species are abundant fossils in parts of the Northland Peninsula (Eagle & Hayward 1992, 1993; Jones 1970; Wakefield 1976), and inferences of paleotemperature support the likelihood that a number of these were reef-forming (Hayward 1977). Cold-water species continued into the Late Miocene and spread over the whole of New Zealand, becoming the dominant element of the Neogene (later Cenozoic) fauna. Squires (1958) also described the history of discovery of New Zealand coral species.

As at the present day, some Tertiary cold-water coral species formed significant thickets or banks. Banks are formed by the continual addition to the substratum of coral debris from a living cap of coral. They can be very long-ranging and support a variety of other invertebrates and fish in life. Particularly
well-developed structures are known from the Wairarapa district from the Late Miocene–Early Pliocene (Squires 1964c). They probably formed at a similar depth and depositional environment as present-day thickets on New Zealand seamounts (c. 400–600 metres).

Zooxanthellate corals formed patch reefs at the Kermadec Islands during Pleistocene time but the dominant framework-building species have since become extinct and there is no contemporary reef formation there (Brook 1998, 1999).

Fossil octocorals include bamboo corals (Isididae) and related species (Squires 1958, 1962a; Hayward 1977), usually as bases and stem fragments. Indeterminate soft corals and a sea pen are also known, as are hydrocorals (Stylasteridae). One of the more intriguing forms is a Paleocene species, Waiparaconus zelandicus, which formed long tubes with a conical arrangement of overlapping bud-like structures at one end. Found in Australia and Antarctica in the Late Cretaceous, and in New Zealand and South America in the Early Tertiary, the tubes were first described as representing a type of stalked barnacle. Buckeridge (1993) reinterpreted Waiparaconus as a possible octocoral related to sea pens.

Features of the New Zealand cnidarian fauna

Fouling and alien species
Cnidarians, especially marine hydrozoans, are among the most significant fouling organisms (Morri & Boero 1986). In New Zealand waters, a number of cnidarian species have been reported fouling vessel hulls, wharf pilings, marine test panels and other anthropogenic surfaces. Ralph and Hurley (1952), Skerman (1958, 1959, 1960), Poore (1968), and Morton and Miller (1968) recorded a number of fouling species, including Amphisbetia bispinosa, Actinothoe albocincta, Campanulina repens, Diadumene nezeelandica, Clytia hemisphaerica (as C. johnstoni), Coryne eximia (as Syncoryne tenella), Culicea rubieola, Ectopleura larynx (as Tubularia), Obelia dichotoma (as O. australis), O. geniculata, Pennaria disticha (as P. australis), Phialella quadrata, Plumularia setacea, Sertularella simplex, and Turritopsis nutricula. Of uncertain identity were species of Diadumene, Flabellum (probably Monomyces), and Halecium. It remains to be determined, however, how many of these species were naturally occurring or adventive. The recent monographs of Schuchert (1996) and Vervoort and Watson (2003) clarify the taxonomic status of the earlier-reported species and list others that, from their distribution around the world, seem candidates for adventism. Based on criteria developed by Chapman and Carlton (1994), 17 species were listed as adventive in New Zealand by Cranfield et al. (1998). In addition to the above, the hydrozoans include Amphisbetia operculata, Bougainvillia muscus, Cladonema radiatum, Clytia linearis, Cordylophora caspia, Coryne japonica, C. pusilla, Ectopleura croce, Eudendrium capillare, Eudendrium ritchei, Gonothyraea loveni, Hartlaubella gelatiosa, Lofecina amirantensis, and Obelia longissima. Anthozoans included the sea anemone Halipanella lineata and, interestingly, two species of scleractinian corals (Hoplangia durotrix and Tethocyathus cylindraceus). At least one of these was considered by Cairns (1991) to have entered New Zealand on ships during or just after the Second World War.

Cnidarians and human health
Cnidarians include some of the most toxic organisms in the sea. In New Zealand waters there are three main stinging species, but most reports are sporadic. The Portuguese man-of-war, or bluebottle (Physalia physalis), frequently washes up on beaches, where inquisitive and unaware young children, attracted by the float and the blue colour of the creature, may touch it and be stung. The lion’s mane jellyfish Cyanea sp. may be encountered by swimmers and snorkellers in summer in harbours and off beaches. In the Hauraki Gulf, hydromedusae and a siphonophore have been implicated in a number of stinging incidents. Popularly known as the
‘long stringy stingy thingy’, the siphonophore is probably *Apolemia uvaria* (Dr Anita Freudenthal pers. comm.). Halstead (1965) and Mackie et al. (1987) have reviewed knowledge of the toxins of these organisms and their effects.

**Ecology and conservation**

The largest seafloor invertebrate on the planet may live in New Zealand waters. Normally when one thinks of cnidarians and conservation, coral reefs come to mind. None of the warm-water species in the Kermadec Islands forms reefs, however, even though they have zooxanthellae. It is in deeper water that New Zealand cnidarians attain large sizes and create three-dimensional habitats occupied by numerous other organisms. A truly huge specimen of the octocoral *Paragorgia arborea* (bubblegum coral) in the collection at NIWA, Wellington, has a trunk with a base 42 centimetres in diameter. It probably attained over seven metres height in its habitat 800 metres deep on the edge of the Campbell Plateau. This would make bubblegum coral the largest seafloor invertebrate known.

Carbon-14 dating was carried out on this specimen, which was obtained by orange roughy (*Hoplostethus atlanticus*) fishers. It yielded an age of 300–500 years (Tracey et al. 2003). A sample was also taken from the densely calcified eight-centimetre-diameter base of a bamboo coral (*Keratoisis*). This gave the same age. Though broken, the specimen probably attained two metres height in life. The most commonly encountered gorgonians on seamounts and other highs are *Paragorgia arborea* and species of *Metallogorgia* and *Keratoisis*. Another large form in New Zealand waters is an undescribed species of *Narella* that attains several metres in height.

In Fiordland, the black coral *Antipathella fiordensis* can attain five metres in height and live for 200–300 years (Grange & Goldberg 1993). Despite their ecological importance, black corals are relatively little studied anywhere in the world, chiefly because of the difficulty of observing them alive in their mostly deepwater habitats. A number of significant studies have been carried out on *A. fiordensis*, however, owing to their accessibility at shallow depths in the fiords beneath a light-excluding layer of tannin-stained brackish water (Grange 1985, 1990; Grange & Singleton 1988; Goldberg et al. 1990; Miller 1997; Parker et al. 1997). It appears that some of the seamount species may be very limited in their distribution, including 12 species restricted to New Zealand waters.

Several scleractinians contribute to deep-water (400–1,400 metres) coral banks, especially on the Chatham Rise and Campbell Plateau, where they are common (Squires 1965) and potentially at threat from any seafloor mining for minerals (Dawson 1984, 2000). The principal frame-builder is *Goniocorella dumosa*, which can attain more than a metre in height. Because colonies form an anastomosing network of branches, the hollow spaces between them provide niches for other corals, such as *Desmophyllum dianthus*, *Stenocyathus vermiformis*, *Flabellum knoxi*, and *Caryophyllia profunda*, as well as many other marine invertebrates. These banks, plus co-occurring stylasterid hydrocorals and antipatharians, are occupied by commercially fished orange roughy. The growth rate of *G. dumosa* is not known, but North Atlantic analogues suggest ages of 200–360 years for metre-high colonies (Wilson 1979; Cairns & Stanley 1982). Scleractinians also co-occur with other large cnidarians (gorgonians, black corals, stylasterids) on seamounts. The habitat three-dimensionality afforded by these large slow-growing cnidarians in deep waters seems correlated with elevated local diversity of invertebrates generally. Deep-water trawls that use large steel bobbins (an entire bobbin rig can weigh over 2 tonnes in water) cause significant damage to these habitats, judging from the variety of large cnidarians taken as bycatch in the early stages of exploitation (Probert et al. 1997). At the very least, the recovery time of these cnidarian-based assemblages must be measured in centuries.

Despite the obvious abundance of medusae and siphonophores in marine
food webs, their predatory role is frequently ignored and no quantitative data are yet available in the New Zealand region. Several studies have demonstrated that medusae are a significant cause of mortality of larvae of caged and wild fish. In recent NIWA studies, hydromedusae and siphonophores are commonly encountered not only in shallow water but have recently been taken in sediment traps suspended 80–400 metres below the surface over the Chatham Rise and more than 400 metres above the seafloor on the Campbell Plateau in water depths of 520 metres and 2,500 metres.

**Symbiosis and parasitism**
The Cnidaria is an ancient phylum and, over the course of geological time, cnidarians have entered into a wide variety of associations with other organisms. Among the most significant is that with symbiotic dinoflagellates (zooxanthellae) and green algae (zoochlorellae). These photosynthetic organisms reside in the tentacles of a number of corals and anemones, and also some hydrozoans and scyphomedusae. Without the metabolites provided by the symbionts, many cnidarians cannot survive. One of the worrying consequences of global warming is that coral reefs may not survive increasing sea temperature. Zooxanthellae exit cnidarian tissues above certain critical temperatures, causing mass mortalities. In temperate New Zealand waters, zooxanthellae are commonly found in intertidal sea anemones, imparting brown and green coloration to many species, and zoochlorellae occur in the freshwater green hydra.

Among other associations, commensal polychaete worms can form galls in stylasterids (Cairns 1991). Polychaetes may induce the formation of calcareous tubes on branches of *Madrepora oculata* and scleractinians *Labyrinthocyathus limatulus* and *Tethycyathus virgatus* can become infested with acrothoracican barnacles (Cairns 1995). The polyp phase of anthoathecates in several families may live in association with other organisms. In the case of the Calycopsidae, this is in the prebranchial cavities of ascidians. In New Zealand, *Bythotiara parasitica* is frequently found in *Pyura rugata*. The species name notwithstanding, the relationship appears to be commensal. No harm is caused to *P. rugata*, and polyps can be cultivated for only a short time outside of the ascidian host (Schuchert 1996). Some soft hexacorals and encrusting hydactiniid hydroids are frequently associated with gastropod shells occupied by hermit crabs. In the case of *Hydractinia novaezelandiae* the association is not obligatory, but *H. rubricata* only lives on shells occupied by *Diacantharus rubricatus* (Schuchert 1996) (see cover photo of Forest et al. 2000). *Hydractinia australis* (Hydactiniidae) also occurs in association with hermit crabs (species not ascertained), whereas *H. bella* (and sometimes the oceanic *Turritopsis rubra*) are found on pigfish (*Congiopodus leucopaeiclis*) (Hand 1961b; Schuchert 1996). Zancleids are often associated with phidoloporid bryozoans. A New Zealand example is *Zancla polymorpha* associated with *Rhynchozozen zealandicum* (as *R. larreyi* in Schuchert 1996). Recently, a primitive new iblomorph barnacle was found in Spirits Bay, northern North Island, attached to the leptotheccate hydroid *Craterithaca novaezelandiae*, the only known host (Buckridge & Gordon 1998). In the plankton, hyperiid amphipods are commonly associated with some medusae (Harbison et al. 1977), as are goose barnacles, but New Zealand records are few and anecdotal.

One of the more remarkable associations documented in recent years is the mutualism between antipatharians and the euryaline ophiuroid *Astrobrachion constrictum*. In Fiordland, *A. constrictum* is obligately associated with *Antipathella fiordensis*, the only antipatharian in this habitat. During a five-year study, the same ophiuroid individuals were observed on the same black coral tree. The snake-stars feed at night, primarily on mucus produced by the host’s polyps but also on planktonic prey captured by the nematocysts. Feeding movements of the ophiuroid arms clear the coral colony of suspended material that might smother it. Observations following natural catastrophic events (e.g. coating of
colonies with sediment from land slips) and transplant experiments showed that survival of *A. fiordensis* is increased if *A. constrictum* is present (Grange 1991).

**Freshwater Cnidaria**

Five freshwater species of hydrozoans have been recorded in New Zealand, mostly cosmopolitan. They comprise two species of Limnomedusae (*Craspedacusta sowerbyi* mostly from North Island volcanic lakes) and *Limnocnida? sp.* from Lake Pupuke, Auckland, and three species of Anthoathecatae. Among the latter are branching, colonial *Cordylophora caspia*, found in brackish to fresh water, and two species of Hydridae. The latter are bright green *Hydra viridissima*—often cited as *Chlorohydra viridissima*—and pale brown to orange *Hydra oligactis* (Marples 1962), but both of these species names need thorough taxonomic investigation based on characters of the cnidae and the egg capsule. The green hydra appears to be fairly widely distributed in New Zealand on aquatic plants. It is often initially encountered on the walls of aquariums stocked with weed from streams and ponds. The brown hydra tends to occur on the undersides of stones in fast-flowing streams. A photograph of the latter species can be seen in Moore (1997).

**Future work**

With 1,126 marine species, the phylum Cnidaria is the third-largest invertebrate group in New Zealand’s seas. Unfortunately, there is not a single full-time cnidarian taxonomist in New Zealand. This dearth of expertise is particularly felt when marine biologists are unable to field the many enquiries the public has each year about jellyfish and other potential marine stingers. But ecological research is also handicapped by the poor knowledge of scyphozoans and siphonophores in the plankton and the difficulty of identifying other cnidarians that live on the seafloor. In the latter environment, the least-known group is the octocorals—185 of the 243 known species are unidentified or undescribed. Fortunately, major progress has been achieved since 1991 by visiting overseas taxonomists who have borrowed museum specimens and published illustrated monographs of New Zealand cnidarians. Monographic work is also under way on several groups, and molecular and morphological studies have begun on some gorgonian genera. The fossil cnidarian fauna is also relatively poorly known, with 92 of the 204 known species uncertain or undescribed.

Apart from taxonomic studies, however, which are necessary to identify and classify the fauna, relatively little is known about the life cycles and ecology of most species. Cnidarians are one of the five major groups of marine-fouling invertebrates of installations and vessel hulls, they feature abundantly in some seafloor assemblages and may dominate ocean plankton at certain seasons when some species swarm. Very few New Zealand studies have been carried out, however. The group also shows promise as a source of useful new biochemicals for antifoulants, neutriceuticals, and biocides. And one never knows when a pure scientific study may turn up a fact of unusual interest or significance to humans. For example, the western Atlantic athecate hydroid *Turritopsis nutricula* has recently been discovered to have a kind of immortality. Its sexually mature medusae are capable of reverting to the immature colonial polyp stage, which in turn can bud new medusae. It achieves this feat through transdifferentiation—altering the differentiated state of a cell by transforming it to another cell type, something that has never been observed in any other metazoan animal but is normal for *T. nutricula* in laboratory culture (Piraino et al. 1996). Is this achievable in New Zealand *T. rubra* (which used to be classified as *T. nutricula*) and what will further studies of *Turritopsis* species yield that could be of potential benefit to understanding how to reverse the ageing process?
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Ordovician Cnidaria
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Checklist of New Zealand living Cnidaria

Marine and freshwater Cnidaria in the following checklist pertain only to those in the Exclusive Economic Zone.

A = alien; E = endemic; endemic genera are underlined; Z = zooxanthellate (subtropical, restricted to the Kermadec Islands); if Z is absent, the species is azooxanthellate; † = new combination. In class Myxozoa, F = freshwater fish host; M = marine fish host.

PHYLUM CNIDARIA

Class ANTHOZOA
Subclass OCTOCORALLIA
Order ALCYONACEA (soft corals)
Alcyonidae

Class MYXOZOA
Subclass ANTHOPLIDAE

Class MOLLUSCA
Subclass NEPTHIDEIDAE

Class ASCIDIA
Subclass SCHIZOCHROMIDA

Class ANTHOZOA
Subclass PENNATULIDA

Class ANTHOZOA
Subclass HIRUDINIDA

Class ANTHOZOA
Subclass ACTINIIDAE

Class ANTHOZOA
Subclass ARISTEIDAE

Class ANTHOZOA
Subclass FLORULIDAE

Class ANTHOZOA
Subclass ACTINIIDAE

Class ANTHOZOA
Subclass TROCHILIDAE

Class ANTHOZOA
Subclass POSIDONIIDAE

Class ANTHOZOA
Subclass SCHIZOCHROMIDA

Class ANTHOZOA
Subclass ACANTHOGORGIDAE

Class ANTHOZOA
Subclass PENNATULIDA

Class ANTHOZOA
Subclass PENTATLIDA

Class ANTHOZOA
Subclass CHROMATIIDA

Class ANTHOZOA
Subclass CYTISCIIDA

Class ANTHOZOA
Subclass TUBULARIIDAE

Order CERIANTHEA (tube anemones)
Order ARACHNANTHEA

Order CERIANTHEA (tube anemones)
Order ARACHNANTHEA

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Order ARACHNANTHEA

Order CERIANTHEA (tube anemones)
Order ARACHNANTHEA
Actinianae
Actinostola
Actinoscyphia
Phymactis polydactyla
Phlyctenactis tuberculosa
Phlyctenactis morrisonii
Oulactis muscosa
Epiactis neozealandica
Epiactis mortenseni
Bunodactis rubrofusca
Bunodactis aucklandica
Bolocera
Aulactinia veratra
Anthopleura rosea
Anthopleura kohli
Anthopleura inconspicua
Actinaria
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
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sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. O. Ocaña
sp. 1 O. Ocaña et al. 2004
sp. 2 O. Ocaña
Carlgren, 1956
Carlgren, 1931
Carlgren, 1924
Silberfeld, 1909
Eltaninactis infundibulum
EPIZOANTHIDAe
Parazoanthus
Paractis monilifera
Halcampactis dubia
Habrosanthus bathamae
Flosmaris bathamae
Oceanactis rhodactylus
Minyas viridula
Liponema multiporum
Limnactinia nuda
Eltaninactis infundibulum
Paracalliactis rosea
sp. D. Opresko
n. sp. D. Opresko
sp. 1 O. Ocaña
sp. 2 O. Ocaña
Order ZOAINTHIDAE
Epizoanthidea
Epizoanthus paguricola
Epizoanthus spp. indet. (5) O. Ocaña
Geraldidea
Gerardia sp. O. Ocaña
Parazoanthidea
Parazoanthus sp. O. Ocaña
Zoanthidea
Isaurus sp. O. Ocaña
Polythoe spp. indet. (2) O. Ocaña
Zoanthus sp. O. Ocaña
Order ANTIPATHARIA (black corals)
Antipathidea
Antipathes cf. chamaearstes Pax & Tschireck, 1932
Antipathes cf. densa Silberfeld, 1909
Antipathes fruticos Gräf, 1857 E
Antipathes cf. gracilis Gräf, 1860
Antipathes cf. grandis Verrill, 1928
Antipathes cf. paucirema Pax & Tschireck, 1932
Antipathes cf. spinulosa (Schultz, 1896)
Antipathes sp. D. Opresko
Cirrhipathes propinquus Brook, 1889
Cirrhipathes spiralis (Linnaeus, 1758)
Cirrhipathes sp. D. Opresko
Stichopathes sarahannoides Van Pesch, 1914
Stichopathes sp. D. Opresko
Aphanipathidae
Acanthopathes undulata (van Pesch, 1914)
Aphanipathes cf. sarahannoides Brook, 1889
Aphanipathes n. sp. D. Opresko
Asteroipathes sp. D. Opresko
Biphipathes cf. colombiana Opresko & Sánchez, 1997
Rhipidipathes cf. reticulata (Esper, 1795)
CLADOPATHIDAE
Cladophates plumosus Brook, 1889
Chrysoipathes tetracanu Opresko, 2003
Cladophates? cf. A. intermedia Brook, 1889
Cladophates sp. D. Opresko
Sibespates n. sp. D. Opresko E
Trissopathes pseudotrichica Opresko 2003
Trissopathes trichita (van Pesch, 1914)
Trissopathes n. sp. D. Opresko E
LEIOPATHIDAE
Leiopathes cf. acanthophora Opresko, 1998
Leiopathes hallae Opresko, 1998
Leiopathes seconda Opresko, 1998
Leiopathes sp. D. Opresko
MYRIOPATHIDAE
Antipathella aperta (Totton, 1923) E
Antipathella fiordensis (Grange, 1990) E
Antipathella strigosa Brook, 1889 E
Antipathella cf. subpinnata (Ellis & Solander, 1786)
Capropsotess sp. cf. abies (Linnaeus, 1758)
Capropsotess sp. cf. cylindrica (Brook, 1889)
Myriopathes catherinei (Pax, 1932)
Myriopathes japonica (Brook, 1889) etchovai (Pax, 1932)
Myriopathes myriophylla (Dallas, 1766)
Myriopathes ules (Ellis & Solander, 1786)
Myriopathes sp. 1 D. Opresko
Myriopathes sp. 2 D. Opresko
Plumapathes cf. fernandezii (Pourtalès, 1874)
Plumapathes sp. penaacea (Dallas, 1766)
SCHIZOPATHIDAE
Bathyipathes alternata Brook, 1889
Bathyipathes conferta Brook, 1889
Bathyipathes patula Brook, 1889
Bathyipathes n. sp. D. Opresko E
Dehodraphyptes cf. A. intermedia Brook, 1889
Dehodraphyptes grandis Opresko, 2002
Dehodraphyptes zooidale Opresko, 2002
Dehodraphyptes n. sp. D. Opresko, 2002 E
Lillipathes lilliei (Totton, 1923) E
Lillipathes n. sp. D. Opresko
Paranipathes helicosticha Opresko, 1999
Paranipathes n. sp. D. Opresko E
Saropathea scoparia (Totton, 1923) E
Saropathea n. sp. D. Opresko E
Schizopathes affinis Brook, 1889
Stauropathes n. sp. D. Opresko E
STYLOPATHIDAE
Stylyphates cf. columnarius (Duchassaing, 1870)
Stylyphates tenergus (Silberfeld, 1909)
Triadipathes cf. triadipathes (Opresko, 1999)
Triadipathes? glutinata Totton, 1923 E
Tylopathes sp. D. Opresko
Order CORALLIMORPHARIA
Corallimorphidea
Corallimorphidae
Conilomorphus profundus Moseley, 1877
Conilomorphus rigidus Moseley, 1877
Corynactis australis Haddon & Duernen, 1896
Corynactis denhartogii Ocaña, 2003 E
Order SCLERACTINIA (stony corals)
Suborder ASTROCOENINIA
ACROPORIDAE
Montipora capricornis Veron, 1985 Z
Montipora spongiosa Bernard, 1897 Z
POCILLIPORIDAE
Madracis kauaiensis Vaughan, 1907
Pocillopora damicornis Linnaeus, 1758 Z
Suborder FURGINA
AGARICIIDAE
Leptoseris scabra
Vernon, 1860
Leptoseris plicata (O. C.observe 1860 Z
Pocillopora damicornis Linnaeus, 1758 Z
Fungiacyathidae
Acanthopathes undulata (van Pesch, 1914)
Aphanipathes cf. sarahannoides Brook, 1889
Aphanipathes n. sp. D. Opresko
Stephanocyathus (O) verbierianus (Alcock, 1902)
Stephanocyathus (Stephanocystis) platypus (Moseley, 1876)
Stephanocyathus (S.) regius Cairns & Zibrowius, 1997
Tethicyathus cylindraceus (Poruțales, 1868)
Tethicyathus cirratus (Alcock, 1902)
Thalampiphyllia bruneum (Brooks, 1877)
Trococytus (Apophyllites) hastatus Bourque, 1903
Trococytus (T.) capula Cairns, 1995
Trococytus (T.) gordonii Cairns, 1995
Trococytus (T.) maculatus Cairns, 1995
Trococytus (T.) rhombocolumna Alcock, 1902
Vaughanella concinna Gravier, 1915
Vaughanella multipilifera Cairns, 1995
FICELLIAE
Falcatoctibulum novogensis Cairns, 1995
Flabellum (Flabellum) arcuatum Cairns, 1999
Flabellum (F.) impressum Squires, 1962
Flabellum (F.) knoxi Ralph & Squires, 1962
Flabellum (Ulloctatus) aureus Squires, 1964
Flabellum (UL) apertum Moseley, 1876
Flabellum (UL) hoffmeisteri Cairns & Parker, 1992
Flabellum (UL) lowekeyesi Squires & Ralph, 1965
Flabellum (UL) messum Alcock, 1902
Flabellum (UL) moseleyi Pourtules, 1880
Javania ficus (Vaughan, 1907)
Javania lampionium (Moseley, 1880)
Monomyces rubrum (Quoy & Gaimard, 1833)
Placocycis siphula Alcock, 1902
Polyocystus welisi Cairns, 1991
Rhizocyathus flabelliformis Cairns, 1989
Tranocystobulum astangentium Cairns & Zibrowius, 1997
Tranocystobulum arcuatum Cairns, 1995
Tranocystobulum dens (Alcock, 1902)
Tranocystobulum paripavoninum (Alcock, 1894)
Tranocystobulum phoenix Cairns, 1995
GARDINERIAE
Gardineria harviensis Vaughan, 1907
Gardineria sp. sensu Cairns 1995
GUYNIIDAE
Pedicocycis keyesi Cairns, 1995
Stenocyathus terniformis (Pourtales, 1868)
Truncatedocystus kermaeensis Cairns, 1989
Truncatedocystus irregularis Cairns, 1989
TURBINOIDEA
Atlotrobium rubescens (Moseley, 1876)
Conocyathus zelandiae Duncan, 1876
Cyathocystus pereus (Alcock, 1902) +
Kionocyathus suteri Diment, 1906
Notocyathus concinna Cairns, 1902
Peponocyathus davisoni Cairns, 1995
Pleotrochus zibrowii Cairns, 1995
Sphenocyathus raphae Squires, 1964
Sphenocyathus siresii Cairns, 1995
Thyrtophycocystus multilobatus Cairns, 1995
SUBORDER DENDROPHYLLEA
DENDROPHYLLEIDAE
Balanophyllia (Balanophyllia) chauds Squires, 1962
Balanophyllia (B.) crassitheca Cairns, 1995
Balanophyllia (B.) diadema Cairns, 1896
Balanophyllia orcutti Alcock, 1902
Balanophyllia paribulum Esper, 1784
Blanodicyathus dunosi (Alcock, 1902)
Hoplonasty suturix Gosse, 1860
Laboratocyathus imitulatus (Squires, 1964)
Laboratocyathus sp. sensu Cairns, 1995
Ocytomoma cicatris Cairns, 1998
Polyocystus norfolkensis Cairns, 1995
Prenocyathus dentiformis (Alcock, 1902)
Solenosmia variabilis Duncan, 1873
Stephanocyathus (Acanthocyathus) spiniger (Marenzeller, 1888)
Stephanocyathus (Odontoocyathus) coronatus (Pourtales, 1867)
Class STAUROZOA (stalked jellyfish)
Order ELEUTHEROCARPIDA
KISHINOUEIDAE
Kishinoueya cf. nagatensis (Oka, 1897)
LIPKEIDAE
Lipea n. sp. L. Gershwin & Gordon
Order CLEISTOCARPIDA
CRATEROLOPHIDAE
Craterolophus macrostomys von Lendenfeld, 1885
DEPASTRIDAE
Depastromorpha africana Carlgren, 1935
Class SCYPHOZOA (jellyfish)
Order CORONATAE
ATOLLIDAE
Atolla parla Russell, 1958
Atolla vaucheani Haeckel, 1880
NAUSITHOIDAE
Pelepyura indicata Vanhoven, 1902
Nausithoe punctata Kolliker, 1853
ORDER SEMPEDSTOMAE
CYANEIDAE
Csranea cf. annulata von Lendenfeld, 1882
Csranea n. sp. L. Gershwin
Dessmonea giudicachi (Lesson, 1829)
Dessmonea n. sp. L. Gershwin
PELAGIIDAE
Dactylometra sp. Gershwin
Pelagia noctiluca (Forsskal, 1775)
Sanderia malayensis Goethe, 1886
ULMARIDAE
Aurelia cf. aurita (Linnaeus, 1758)
Aurelia cf. maldiviensis Bigelow, 1904
Aurelia cf. labiata Chamisu & Esyendhardt, 1821
Aurelia cf. coerulescens von Lendenfeld, 1885
Phaeophila cameratia Brandt, 1835
ORDER RHIZOSTOMAE
ARCHIRHIZIDAE
Archihriza aurora Haeckel, 1880
Auroria cormea Haeckel, 1880
CASSIOPEIDAE
Toreuma daphne (Peron & Lesueur, 1810)
CATOSTYLIDAE
Leptobrachia leptops (Chamisu & Esyendhardt, 1821)
[as Leponoa leptura Haeckel, 1880]
MASTIGIDAE
Phyllorhiza punctata von Lendenfeld, 1885
CLASS CUBOZOA (box jellies)
Order CUBOMEDUSAE
CARYBDEIDAE
Carybdea stokstii Stokstii, 1926
CLASS HYDROZOA
Subclass TRACHYLINA
Order LIMNOCOMIDAE
LIMNOCIDAE
Limoncidae? sp. Schuchert in litt. L. Pupuke
FAMILY DIAPERIDAE
Craspedacusta sowerbyi Lancaster, 1880 F
Order LAINGIOMEDUSAE
LAINGIIDAE
Fabiana sphaerica Schuchert, 1996
Order NARCOMEDUSAE
AEGINIIDAE
Lytocarpia vulgaris Vervoort & Watson, 2003 E
Lytocarpia sp. Vervoort & Watson, 2003
Macroceraria phoenica (Busk, 1852)
Monosorius banksi (Gray, 1843)
Monosorius ?penarius (Linnaeus, 1758)
Wanglaophoria rostrifrons Vervoort & Watson, 2003 E

CAMPANULINIDAE
Opercularia minutum (Bale, 1924)
Tripora arboresum Hirohito, 1995

CIRRHOTOVENIDAE
Cirrhiolochia polyneura Kramp, 1959

CLATHROZOIDAE
Clathrozoa sp. Vervoort & Watson 2003

FIRENIDAE
Eirene celenousis Browne, 1905
Eirene menoni Kramp, 1953
Eirene proboscidea Bouillon & Barnett, 1999 E
Eirene tenus (Browne, 1807)
Eutina curua Browne, 1905
Eutina mira McCrady, 1859

EUCHEILOTIDAE
Euchelium tomentosum Busch, 1851

Haleciidae

Halicornopsis elegans
Hebellopsis scandens
Anthohebella parasitica
Halopteris prominens
Halopteris minuta
Halopteris crassa
Corhiza splendens
Antennellopsis integerrima

Haleciina

Eucheilota tropica
Eucheilota menoni

Euchilotea

Halecium plicatocarpum
Halecium lenticulare
Halecium fragile
Halecium delicatulum
Halecium corrugatissimum

Mitrocomidae

Mitrocomella niwai
Cosmetirella davisi

MALAGAZIIDAE
Zygophylax unilateralis
Zygophylax sibogae
Zygophylax polycarpa
Zygophylax binematophoratus
Zygophylax polypodia

MITROCOMIDAE
Mitrocomella niwai
Cosmetirella davisi

NEW ZEALAND INVENTORY OF BIODIVERSITY

Eurygaster

Sminthea eurygaster
Rhopalonema funerarium
Persa incolorata
Pantachogon haeckeli
Crossota brunnea

Aequorea forskalea
Aequorea australis

Aglaophenia hystrix
Aglaophenia digitulus
Aglaophenia ctenata
Aglaophenia acanthocarpa

Filellum

Filellum sp. Vervoort & Watson 2003

PLUMULARIAE

Gonaxia intercalata
Gigantotheca raukumarai
Dictyocladium thuja
Dictyocladium monilifer
Dictyocladium amplexum
Crateritheca novaezelandiae

Campanulidae

Amphisbetia minima
Amphisbetia fasciculata
Plumularia spirocladia
Plumularia setacea
Plumularia insignis
Plumularia filicula
Plumularia congregata
Plumularia caliculata
Plumularia brachiata
Plumularia anonyma Vervoort & Watson, 2003 E
Plumularia brachiata Totton, 1930 E
Plumularia caliculata Bale, 1888
Plumularia conglobata Vervoort & Watson, 2003 E
Plumularia filicula
Plumularia insignis Allman, 1883
Plumularia opinia Bale, 1924 E
Plumularia setacea (Linnaeus, 1758) A
Plumularia setacea E
Plumularia spirocladia Totton, 1930 E
Plumularia tenessonii Totton, 1930 E
Plumularia wettii Bale, 1887

SERTULARIIDAE

Amphistheta bispinosa (Gray, 1843)
Amphistheta episopus (Allman, 1876)
Amphistheta fasciata (Kirchenpauer, 1864) E
Amphistheta minima (Thompson, 1879)
Amphistheta opercularis (Linnaeus, 1758 A
Amphistheta trispinosa (Coughtrey, 1875)
Ctenotheca bidens Vervoort & Watson, 2003 E
Ctenotheca bilabia (Bale, 1912)
Ctenotheca insignis (Thompson, 1879)
Ctenotheca novaeezelandiae (Thompson, 1879) E
Ctenotheca zelandica (Gray, 1843) E
Dictyocelium adunum Vervoort & Watson, 2003
Dictyocelium monilifer (Hutton, 1873) E
Dictyocelium reticulatum (Kirchenpauer, 1884)
Dictyocelium thunbergii Vervoort & Watson, 2003 E
Dictyocelium asteraceum (Vervoort, 1993)
Diphasis sulcata (Busk, 1852)
Gigantotheca maximus Vervoort & Watson, 2003
Gigantotheca raukumarai Vervoort & Watson, 2003 E
Gonaxia australis Vervoort & Watson, 2003 E
Gonaxia constructa (Totton, 1930) E
Gonaxia impressa Vervoort & Watson, 2003 E
Gonaxia intercalata Vervoort & Watson, 2003 E

Lafea dufresnei (Fleming, 1820)
Lafea aurantiensis (Millard & Bouillon, 1973) A
Zygophylax binauralis Vervoort & Watson, 2003 E
Zygophylax cervicornis (Nutting, 1905)
Zygophylax polyopodius Vervoort & Watson, 2003 E
Zygophylax pseudofalcatus Vervoort & Watson, 2003 E
Zygophylax sibogae Billard, 1924
Zygophylax tensa Williams, 1890
Zygophylax unilateralis Totton, 1930

LAODICEIDAE
Laodicea indica Browne, 1905
Staurodiscus goeti (Uchida, 1927)
Tentaculum polyneura Kramp, 1959
LOVENELLIDAE
Lovenella assimilis (Browne, 1905)
Lovenella sp. Vervoort & Watson 2003

MALAGAZIIDAE
Malagazia carolinensis (Mayer, 1900)
Octotrichiaceum indicum Kramp, 1958

MITROCOMIDAE
Cosmetrella davisii (Browne, 1902)
Mitrocomella brownei (Krapf, 1930) E
Mitrocomella frigida (Browne, 1910)
Mitrocomella niveaou Bouillon & Barnett, 1999 E
PHALELLIDAE
Phialella fallaciosa Browne, 1902
Phialella quadrata (Forbes, 1848)
Plicotheca anitae Calder & Vervoort, 1996

PLUMULARIAE
Monotheca epibracteolosa Watson, 1973
Monotheca hialina (Bale, 1882)
Monotheca pulchella (Bale, 1882)
Monotheca spirocladia (Bale, 1882)
Monotheca togata Watson, 1973
Monotheca sp. Vervoort & Watson 2003
Nemertesia ciliata Bale, 1914
Nemertesia cymodocea (Busk, 1851)
Nemertesia elongata Totton, 1930 E
Nemertesia novissimae Vervoort & Watson, 2003 E
Nemertesia sp. Vervoort & Watson 2003
Plumularia anomala Vervoort & Watson, 2003 E
Plumularia brachiata Totton, 1930 E
Plumularia cernigata Vervoort & Watson, 2003 E
Plumularia filicula
Plumularia insignis Allman, 1883
Plumularia opinia Bale, 1924 E
Plumularia setacea (Linnaeus, 1758) A
Plumularia setacea E
Plumularia spirocladia Totton, 1930 E
Plumularia tenessonii Totton, 1930 E
Plumularia wettii Bale, 1887

SEKTULARIIDAE

Amphistheta bispinosa (Gray, 1843)
Amphistheta episopus (Allman, 1876)
Amphistheta fasciata (Kirchenpauer, 1864) E
Amphistheta minima (Thompson, 1879)
Amphistheta opercularis (Linnaeus, 1758 A
Amphistheta trispinosa (Coughtrey, 1875)
Ctenotheca bidens Vervoort & Watson, 2003 E
Ctenotheca bilabia (Bale, 1912)
Ctenotheca insignis (Thompson, 1879)
Ctenotheca novaeezelandiae (Thompson, 1879) E
Ctenotheca zelandica (Gray, 1843) E
Dictyocelium adunum Vervoort & Watson, 2003
Dictyocelium monilifer (Hutton, 1873) E
Dictyocelium reticulatum (Kirchenpauer, 1884)
Dictyocelium thunbergii Vervoort & Watson, 2003 E
Dictyocelium asteraceum (Vervoort, 1993)
Diphasis sulcata (Busk, 1852)
Gigantotheca maximus Vervoort & Watson, 2003
Gigantotheca raukumarai Vervoort & Watson, 2003 E
Gonaxia australis Vervoort & Watson, 2003 E
Gonaxia constructa (Totton, 1930) E
Gonaxia impressa Vervoort & Watson, 2003 E
Gonaxia intercalata Vervoort & Watson, 2003 E
Tiaropsis hicksoni
Tiaropsis gordoni
Tiaropsidium roseum
Stegolaria irregularis
Modeeria rotunda
Synthecium tottoni
Synthecium protectum
Synthecium megathecum
Tasmanaria pacifica
Symplectoscyphus tuba
Symplectoscyphus spiraliformis
Symplectoscyphus rentoni
Symplectoscyphus procerus
Symplectoscyphus paulensis
Symplectoscyphus johnstoni subtropicus
Symplectoscyphus johnstoni johnstoni
Symplectoscyphus irregularis
Symplectoscyphus fuscus
Symplectoscyphus columnarius
Symplectoscyphus amoenus
Sertularia unguiculata
Sertularia tumida
Sertularella gayi gayi
Sertularella diaphana
Sertularella crassiuscula
Sertularella areyi
Salacia farquhari
Salacia desmoides
Salacia bicalycula
SyNTheseIIDAe
2003 e
2003 e
?
sp. 1 Vervoort & Watson 2003 e
edentula
megalotheca
Jäderholm, 1896
(Lamouroux, 1816)
Allman, 1872
Vervoort & Watson, 2003 e
Vervoort & Watson, 2003 e
Jäderholm, 1903
Busk, 1852
Coughtrey, 1876
Allman, 1888
Vervoort & Watson, 2003 e
Vervoort & Watson, 2003 e
Jäderholm, 1903
(Bale, 1924) e
Kramp, 1932
Fewkes, 1882
(Trebilcock, 1928) e
TOTTON, 1930 e
Stechow, 1923
Allman, 1888
Vervoort & Watson, 2003 e
Vervoort & Watson, 2003 e
(A. Agassiz & mayer, 1899)
(A. Agassiz, 1849)
(L. Agassiz, 1836)
(A. Agassiz & mayer, 1899)
(L. Agassiz, 1836)
(A. Agassiz & mayer, 1899)
(L. Agassiz, 1836)
(A. Agassiz & mayer, 1899)
(L. Agassiz, 1836)
(A. Agassiz & mayer, 1899)
(L. Agassiz, 1836)
(M. Sars, 1882)
Malek, 1967

Amphinema rugosa
Amphinema dinema
Hydractinia rubricata
Hydractinia otagoensis
Hydractinia novaezelandiae
Hydractinia minuta
Hydractinia bella
Hydractinia australis
Eudendrium terraenovae
Eudendrium ritchiei
Eucodonium brownei
Calycopsis bigelowi
Bythotiara
Bythotiara murrayi
Cytaeis
cytaeis tetrastyla
Clathrozoella bathyalis
Koellikerina maasi
Garveia
Dicoryne conybearei
Bougainvillia vervoorti
Bougainvillia macloviana
Bougainvillia inaequalis
Suborder FILIFera
Tulpa diverticulata
Silicularia rosea
Orthopyxis mollis
Orthopyxis integra
Orthopyxis crenata
Orthopyxis affabilis
Obelia geniculata
Hartlaubella gelatinosa

Conopora verrucosa (Studer, 1878) "Cnephea" antedonaria Cairns, 1991 e
Cnephea fragilis Cairns, 1991 e
Cnephea sertularia Cairns, 1991 e
Cnephea corysma Cairns, 1983
Cnephea fragilis Cairns, 1983
Cnephea polypoma Cairns, 1991 e
Cnephea robusta Cairns, 1991 e
Cnephea studeriana Stechow, 1923 e
Dichotophora dispar Cairns, 1991 e
Dichotophora violacea (Pallas, 1766)
Errina bicolor Cairns, 1991 e
Errina chathamensis Cairns, 1991 e
Errina cheloperca Cairns, 1983 e
Errina cook Hickson, 1912 e
Errina denudata Hickson, 1912 e
Errina gnacis Marenzeller, 1903
Errina hicksoni Cairns, 1991 e
Errina laeavigata Cairns, 1991 e
Errina novaezelandiae Hickson, 1912 e
Errina reticulata Cairns, 1991 e
Errina sinuosa Cairns, 1991 e
Inferiolabia labiata (Moseley, 1879)
Inferiolabia loesi (Cairns, 1893)
Inferiolabia spinosa Cairns, 1991 e
Lepidopora cryptocorys Cairns, 1985 e
Lepidopora dendrostylus Cairns, 1991 e
Lepidopora microstylus Cairns, 1991 e
Lepidopora polystylophora Cairns, 1985 e
Lepidopora sarmentosa (Boschma, 1968) e
Lepidopora symmetrica Cairns, 1991
Lepidopora altispina Cairns, 1991
Lepidopora cervicornis (Brock, 1942) e
Lepidopora chauliostylus Cairns, 1991 e
Lepidopora fasciolaris (Cairns, 1893)
Lepidopora robusta Cairns, 1991 e
Lepidopora antedonaria (Hickson & England, 1905)
Spurred microycladum Cairns, 1991 e
Spurred microycladum Cairns, 1991 e
Stenohelia conferta
Pseudocrypthelia pachypoma
Stylaster imbricatus
Stylaster eguchii
Stylaster brumus
Stylaster reticulata
Errina novaezelandiae
Errina laevigata
Errina dendyi
Errina cooki
Errina chathamensis
Errina bicolor
Crypthelia polypoma
Crypthelia cymas
Conopora verrucosa
Conopora unifacialis
Conopora laevis
Conopora candelabrum
Calyptopora
Adelopora crassilabrum
STyLASTerIDAe
Rathkea octopunctata
Halitiara formosa
PROBOSCiDACTyLIDAe
Pandeopsis ikarii
Neoturris papua
Leuckartiara
Leuckartiara octona
Leuckartiara annexa
Leuckartiara octona
Leuckartiara sp. 1
Leuckartiara sp. 2
Merga sp. NWA P Schuchert
Neoturris papua
Panrea conica
Quoy & Gaimard, 1827
Pandeopsis ikarii (Uchida, 1927)
PROBOSCiDACTyLIDAe
Pandeopsis sp.
PROTARIADe
Halitiera formosa
Halitiera inflensa
RATHEKIDe
Radiataformis M. Sars, 1835
Radiata octopunctata (M. Sars, 1835)
STYLASTERIDAe
Adelopora crassilabrum Cairns, 1991 e
Adelopora fragilis Cairns, 1991 e
Asta aspeditopena Rahmsen, 1968 e
Calyptraea reticularis Bohsche (Boschma, 1966)
Calyptraea sertularia Cairns, 1991 e
Conopora corysma Cairns, 1991 e
Conopora gigantea Cairns, 1991 e
Conopora laceris (Studer, 1878)
Conopora tetracladum Cairns, 1991 e
Conopora antedonaria Cairns, 1991 e
Conopora verrucosa (Studer, 1878)
"Cnephea" antedonaria Cairns, 1991 e
Cnephea corysma Cairns, 1983
Cnephea fragilis Cairns, 1983
Cnephea polypoma Cairns, 1991 e
Cnephea robusta Cairns, 1991 e
Cnephea studeriana Stechow, 1923 e
Dichotophora dispar Cairns, 1991 e
Dichotophora violacea (Pallas, 1766)
Errina bicolor Cairns, 1991 e
Errina chathamensis Cairns, 1991 e
Errina cheloperca Cairns, 1983 e
Errina cook Hickson, 1912 e
Errina denudata Hickson, 1912 e
Errina gnacis Marenzeller, 1903
Errina hicksoni Cairns, 1991 e
Errina laeavigata Cairns, 1991 e
Errina novaezelandiae Hickson, 1912 e
Errina reticulata Cairns, 1991 e
Errina sinuosa Cairns, 1991 e
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Inferiolabia spinosa Cairns, 1991 e
Lepidopora cryptocoryn Cairns, 1985 e
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Lepidopora polystylophora Cairns, 1985 e
Lepidopora sarmentosa (Boschma, 1968) e
Lepidopora symmetrica Cairns, 1991
Lepidopora altispina Cairns, 1991
Lepidopora cervicornis (Brock, 1942) e
Lepidopora chauliostylus Cairns, 1991 e
Lepidopora fasciolaris (Cairns, 1893)
Lepidopora robusta Cairns, 1991 e
Lepidopora antedonaria (Hickson & England, 1905)
Spurred microycladum Cairns, 1991 e
Spurred microycladum Cairns, 1991 e
Stenohelia conferta Boschma, 1968 e
Stephanohelia praeclara Cairns, 1991
Stylaster brumus Boschma, 1970
Stylaster eguchi (Boschma, 1968)
Stylaster gracilis Milne Edwards & Haim, 1850 e
Stylaster horologium Cairns, 1991 e
Stylaster inbricatina Cairns, 1991 e

PHYLUM CNIDARIA
97
Suborder CAPITATA
BOEROMEDUSIDAE E
BOROMEDUSA EURUCOYXIA Bouillon, 1995 E
CANDIALBRIDAE
Candelabrum austral (Briggs, 1928)
CLADOCCYRIDAE
Cladocoryne flexo Oseth, 1871
CLADONEMATIDAE
Cladonema radiatum Dajardin, 1843 A
CORYMORPHIDAE
Corynophora forbesi (Mayer, 1894)
Corynophora furcata (Krapf, 1848)
CORYNIDAE
Corne eximia Allman, 1859 A
Corne japonica (Nagao, 1962) A
Corne pusilla Gaertner, 1774 A
Corne tricula Schuchert, 1996
Corne sp. 1 Schuchert 1996
Corne sp. 2 Schuchert 1996
Dipurena sphaerogaster Haeckel, 1879
ELEUHERIDAE
Staurocladia vallentini Browne, 1902
Staurocladia wellingtoni Schuchert, 1996
EUPHYLLIDAE
Ephypra problematica Schuchert, 1996
HYDRIDAE
Hydra viridissima Schuchert 1996
Hydra oligactis Pallas, 1766 F
MARCELOPSIDAE
Phegophora minulis Dendy, 1902 E
OCEANIDAE
Cordylophora caspia (Pallas, 1771) A F
Cordylophora neptunia (Linnaeus, 1758)
Veleva veleva (Linnaeus, 1758)
SOLANDERIDAE
Solenidra secunda (Inaba, 1892)
Solenidra secunda minima (Hickson, 1903)
Solenidra ericopsis (Carter, 1873)
TUBULARIDAE
Ectopleura crocea (L. Agassiz, 1862) A
Ectopleura larvina (Eills & Solander, 1786) A
Ectopleura minori Mayer, 1910
Ectopleura multicirrata Schuchert, 1996
Hybocodon prolifer L. Agassiz, 1862
ZANCLIDAE
Zanclaea polynorma Schuchert, 1996
Order SIPHONOPHORA
Suborder CYSTONECTIDAE
Physalia physalis Linné, 1758
Suborder PHYSONECTIDAE
AGALMIDAE
Agula elegans (Sars, 1846)
Agula okeni Eschscholtz, 1825
Cordaquina cordiforme Totton, 1932
Halistemma rubrum (Vogt, 1852)
Marrus antarcticus Totton, 1954
Marrus oceana (Moser, 1925)
APOLEMIIDAE
Apolemia auraria (Lesueur, 1817)
PHYSOPHORIDAE
Physophora hydrostica Forskål, 1775
PYROSTEPHIDAE
Bargmannia sp.

New Zealand inventory of biodiversity

98

New combinations and changes to recent monographs

Order SCLERACTINIA: changes to list in Cairns (1995):
Carposiphonia elongata renamed C. crosnieri.
Carposiphonia compressa now considered a junior synonym of Premosphaera densiformis.
Cryptothecus venustus sensu Cairns (1995) now described as Plectothecus zibrowii.
Deltocyathus formosus now considered a junior synonym of D. sulcansense.
Flabellum angustum sensu Cairns (1995) now described as F. asciticula.
Jasania pachythea now considered a junior synonym of J. fusca.
Tropocyathus plicae was transferred to Cyathothecus.
Vughaella oceanoi now considered a junior synonym of V. cavernosa.

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Checklist of New Zealand fossil Cnidaria

Taxa listed by Hinde and Holmes (1892) are problematic in many cases. Where their genus assignments can today be attributed to more than one genus on the basis of spicules, they are not included in the checklist below. Only named species and those generic assignments easily recognised by particular microscleres or megascleres are included.

E = endemic species; * = new record. Fossil species are followed by ranges using the standard abbreviations for the New Zealand Geological Timescale (except Rec = Recent).

Paleozoic

Compiled by Hamish J. Campbell and Anthony J. Wright, and partly based on Shirley (1938), Hill (1952, 1955), Leed (1955), and Waterhouse (1979, 1986).

N = North Island; S = South Island. O = Ordovician; D = Devonian; P = Permian.

Mesozoic


C = Chatham Islands; N = North Island; S = South Island. K = Cretaceous; J = Jurassic; (L)Tr = (Lower) Triassic.
Cenozoic


C = Chatham Islands; K = Kermadec Islands; N = North Island; S = South Island.
Z = zooxanthellate taxa. E = Early; M = Middle; L = Late; Fl = Flies; Pi = Piocenes; Mio = Miocene; Oli = Oligocene; Eoc = Eocene; Pal = Paleocene.

NEW ZEALAND INVENTORY OF BIODIVERSITY

PHYLUM CNIDARIA
Class ANTHOZOAA
Subclass OCTOCORALLIA
Order ALCYONACEA
CORALLIIDAE?
Gen. et spp. indet. SC EEOc–Lmio
SIDIDAE?
Ais dactyla Tenison-Woods, 1880 S EOLi–Lmio
Keratocystis tangents Grant, 1976 N Lmio–Rec
Molikia advena Squares, 1958 S EOLi
PARISIDIDAE
Parisis fraxinum Verrill, 1864 N Lmio
Parisis hamiltoni (Thompson, 1908) NS LOli–Lmio
Order PENNATULACEA
PENDULLIDAE
Graphulidaria longissima Squares, 1958 S LEoc–Emio
Order INCERTAE SEDIS
WAIKACONIDAE
Waisparacornus zelandicus (Withers, 1951) LEOc
Order SCLERACTINIA
Suborder ASTROCOeniNa
ACROPORIDAE
Acropora dianorca (Dana, 1846) ZK EPLRec
Astreopora cf. heddastetleri Reuss, 1866 ZN EMOi
Montipora sp. ZK EPLRec
ASTROCOeniNa
Styloscionellia guentherti Bassett-Smith, 1890 ZK EPLRec
POCILPORIDAE
Madracis dodecachora Squares, 1958 S EEOc
Pocillopora damicornis (Linnaeus, 1758) ZK EPLRec
Pocillopora ?seggaz Edwards & Haime, 1860 ZK EPLRec
Stylphora pistillata (Esper, 1897) ZN EMio
Suborder FUNGIINa
AGARICIDIDAE
Cytalthusia sp. ZN EMio
Gardineroseris planulata (Dana, 1846) ZK EPLRec
Leptoseris setae (Filaci & Scheer, 1976) ZK EPLRec
Leptosoria sp. ZN EMio
Porotuna maldivensis (Gardiner, 1905) ZK EPLRec
Poruna minuta Wells, 1954 ZK EPLRec
FUNGIIDAE
Cycloteris ?vaughani (Boschma, 1923) ZK EPLRec
Discosoma australis Squares, 1958 S MEoc
Discosoma aff. asterites Squares, 1958 N EMio
PECTINIDIDAE
Funghyllia sp. N EMio
PORTIDIDAE
Alveopora polycantha Reuss, 1867 ZN EMio
Alveopora sp. Dana, 1846 K EPLRec
Dictyopora sp. ZN EMio
Goniopora sp. ZN EMio
Goniopora sp. ZK EPLRec
Porites sp. ZN EMio
Porites sp. ZK EPLRec
SIDERASTREIDAE
Coscinura columnata (Dana, 1846) ZK EPLRec
Suborder FAVINa
FAVIIDAE
Cyphastrea sp. ZN EMio
Cyphastrea serulata (Forskål, 1775) ZK EPLRec
Favia ?spectosa (Dana, 1846) ZK EPLRec
Favites flexuosa (Dana, 1846) ZK EPLRec
Favites sp. ZK EPLRec
Goniastrea aurealensis (Edwards & Haime, 1857) ZK EPLRec
Goniastrea sp. ZN EMio
Leptastrea sp. ZN EMio
Leptotyphlogorgia (Edwards & Solander, 1786) ZK EPLRec
Montastrea curta (Dana, 1846) ZK EPLRec
Montastrea sp. ZN EMio
Odulophyllia crispa (Lamarck, 1816) ZN EMio
Platygyra sp. ZN EMio
MERULIDINa
Hydnophora pilosa Veron, 1895 ZK EPLRec
Hydnophora sp. ZN EMio
MUSsIDa
Acanthophyllia? sp. ZN EMio
Labophyllia sp. ZK EPLRec
Scyphium australis Milne Edwards & Haime, 1849 ZK EPLRec
SPECIALIZED CORALS
MADRADeA
Madrapora granulata (Tenison-Woods, 1880) NSC EEOc–Lmio
MERMATIONa
Onchina oamaruensis Park, 1917 SEoEo–EMio
Onchina virens Squares, 1958 NC EMio–Rec
RHIZANGIIda
Astrangia (Coenangia) sp. N Ple
Cladanga sp. ZN EMio
Culicina rubroca (Quoy & Gaimard, 1833) N ?PLiRec
Culicina ?rubroca (Quoy & Gaimard, 1833) K EPLRec
Oulangia radames Squares, 1960 N Lmio–PLi
Platyheilia distans Tenison-Woods, 1880 NS E–Lmio
Rhiangia atorareva Squares, 1962 S LOli–EMio
Suborder CARBYPHYLLIa
CARBYPHYLLIDa
Astronemia liaquatula Squares, 1958 S MEoc
Caryophyllia clavus coronata (Tenison-Woods, 1880) NS E–Lmio
Caryophyllia c. zelandiae Squares, 1958 NS L–EoEoc
Caryophyllia japonica Marenzeller, 1888 N EMio–PLi
Caryophyllia lankelifere Moseley, 1881 N EMio
Caryophyllia cf. lankelifere Moseley, 1881 S MMio
Caryophyllia profunda Moseley, 1881 S PLi–Rec
Ceratophyllum (Conotrochus) cf. typus australiensis
Duncan, 1870 S ?EMio
Ceratophyllum exiguus Squares, 1958 S EMio
Ceratophyllum cf. rubescens (Moseley, 1881) C
Ceratophyllum sp. N EMio
Dasmosomita? spissa Squares, 1958 S Crest/Pal
Desmophyllia sp. S MEoc
Labyrinthophyllia periallus (Squires, 1962) S LOli–EMio
Lochtmaerotrochus micromatatus Squares, 1962 S PLi–EoEoc
Leptophyllia parvisperata (Tenison-Woods, 1880) NS M–LOli–PLi
Stephanocyathus acinetocathus mantelli (Milne-Edwards & Haime, 1857) NS E–LOli–MMio
Stephanocyathus (A.) spiniger (Marenzeller, 1888) S MEoc–Rec
Stephanocyathus (Odontocyathus) irix Squares, 1958 NS E–LOli
Tethycyathus palicus Squares, 1962 S EMio
Tachycyathus lemmisquatus (Squires, 1958) S P–LEoEoc
Tachycyathus (Aplocyathus) papaoresis (Clarke, 1905) NS EMio
Tachycyathus (?Platyctyathus) powelli Squares, 1962 S EMio
FLABELLIDa
Conosomiila? sp. N EMio
Flabellium circularia Tenison-Woods, 1880 S EMio
Flabellium lamellolam Alcock, 1902 N EMio
Flabellium laticostatum Tenison-Woods, 1880 S LOli
Flabellium mariae Tenison-Woods, 1880 N ?Pli–Ple
Flabellium paxoniium Lession, 1831 NS LOli–EMio
Flabellium radians Tenison-Woods, 1880 S LOli–Rec
Flabellium sp. N EMio
Flabellium (Ulocyathus) planus Squares, 1962 S EMio
Flabellium (?Ulocyathus) sp. N S MEoc–LOli
Flabellium (?Ulocyathus) sp. B N EMio
Monomycys rubrum (Quoy & Gaimard, 1833) NS LMio–Rec
Monomycys cf. rubrum (Quoy & Gaimard, 1833) N EMio
Tortoflabellum feninig Squares, 1958 NS E–LOli–Rec
Tortoflabellum maraxici Squares, 1962 S EMio
Truncatoflabellum sphenoides (Tenison-Woods, 1880) S MEoc–MMio
Truncatoflabellum sp. A N EMio
Truncatoflabellum sp. B N EMio
Truncatoflabellum sp. C N EMio
Truncatoflabellum sp. D N EMio
Truncatoflabellum sp. E N EMio
Truncatoflabellum sp. F N EMio
STENOCAThIDa
Stenocyathus vermiciformis (Bourarta, 1868) N EMio–Rec
Truncatagynia aff. irregularis Cairns, 1989 S N EMio–Rec
TURBINidiA
Cenoagynia zelandiae Duncan, 1876 S MEoc–Rec
Deltocyathoides australiensis (Duncan, 1870) NS LOli–Lmio
Deltocyathoides pedicillaris (Tenison-Woods, 1880) NS ?Mli–MMio
Deltocyathoides? caespitulos (Squires, 1958) S EMio
Deltocyathoides? sp. N EMio (as Notocyathus conicus)
Idiactyocyst sp. N EMio
Notocyathus caecuuscis Squares, 1962 NS LOli–MMio
Peporocyathus minimus (Yabe & Eguchi, 1937) NS LOli–EMio
Sphenocyathus aschistus Squares, 1958 S ?MMio
Sphenocyathus laticostatus Squares, 1962 S L–LOli
Sphenocyathus sulphatus Squares, 1964 NC EPLRec
Sphenocyathus sp. A S Oli
List of changes to fossil taxon names

The taxon name at left appears in the checklist of fossil species above, followed by its previous attribution in the literature. In square brackets is the author of the new attribution, or it is introduced here for the first time.

Acantophyllia? sp.: Squires 1958 as Lobophyllia sp. cf. L. japonica [Brook 1983].
Crissatophyllus exigus: Squires, 1958 as Conrotrochus [Wells 1977].
Crissatophyllus sp.: Eagle & Hayward 1992 as Cyathoceras.
Cyclostrea sp: Squires 1962a as Cyclostrea sp. cf. C. chalcidicum [Hayward 1977; Brook 1983].
Deltoxyathoides? cuspidatus: (Squires, 1958) as Notocyathus (Paradeltoxyathus) [Cairns 1997].
Deltoxyathoides? sp.: Squires 1958 as Notocyathus conicus part; Cairns 1989 as Pemonoxyathus sp.
Enallopsammia sp.: Squires 1958 [not a dendrophyllid according to Cairns 2001, p. 34].
Flabellum circulare: Squires 1958 as F. pavoninum circulare part [Cairns 1989].
Flabellum laticotostatum: Squires 1958 as F. pavoninum distinctum part [Cairns 1989].

Dendrophyllia sp. C LPli/EEoc
Euglyptosamnia japonica Rehbberg, 1892 NSC EMio–Rec
Enallopsamnia sp. NS E-MMio
Endopachys cf. grayi Müll–Edwards & Haim, 1848 N EMio
Endopamnia? sp. sp. EMio
Rhizysammia cf. verrilli van der Horst, 1922 K EPl
Turbinaria radialis Bernard, 1896 ZK EPl–Rec
Turbinaria sp. ZN EMio
Turbinaria sp. ZK EPl

Class HYDROZOA
Subclass HYDROIDOLINA

Order ANTHOATHECATA
AXOPORIDAE
Axopora clavata (Squires, 1958) S LMio
STYLASTERIDAE
Calyptopora cf. reticulata Boschma, 1968 N Mio
Conopora cf. laevis (Studer, 1876) N Mio
Errina sp. Cairns & Grant–Mackie, 1993 C Eoc
Inferiophyllia cf. labiata (Moseley, 1879) N Mio
Lepidopora sp. Cairns & Grant–Mackie, 1993 S Moli
Sporadopora marginata Tenison–Woods, 1880 C LPli
Sporadopora ?mortensi Broch, 1942 N EPli
Stylaster gigas Cairns & Grant–Mackie, 1993 S Moli

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